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THE GENERA OF CYPERACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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CYPERACEAE A. L. de Jussieu, Gen. Pl. 26. 1789, nom. cons.

(SEDGE FAMILY)

Small to large perennial or annual herbs of aquatic or terrestrial habitats. Roots fibrous; many species rhizomatous or stoloniferous. Plants glabrous or

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Preceding the reference for each genus, a paragraph is given listing by author all familial or tribal references pertinent to that genus.

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The illustrations were prepared by Karen Stoutsenberger under the supervision of Carroll Wood or Kenneth R. Robertson, from plants collected by Carroll Wood or from specimens in the herbaria of Harvard University (A, GH).

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scabrellate. Culms single, approximate, or caespitose, trigonous, triquetrous, or terete, the cortex chlorenchymatous, the central region aerenchymatous or hollow; cortical bundles with sheaths like those in the leaves. Leaves basal or both basal and cauline; sheaths closed; blades linear to lanceolate, flat, conduplicate, plicate, or involute; stomata paracytic, sometimes surrounded by 1–4 porrect or arching cuticular papillae; anatomy non-kranz or kranz, if kranz, the bundle sheaths 2-layered ("*Cyperus* type") or 3-layered ("*Fimbristylis* type"). Inflorescences spicate or umbelliform [corymbose], sessile, simple, or with second- and third- [to fifth-]order branching. Spikelets 1- to many-flowered, basally subtended by a scalelike prophyll, above which may be 1 or more sterile scales; flowers perfect or imperfect and monoecious (rarely dioecious), each borne in the axil of a scale ("glume" of some authors), anemophilous (infrequently entomophilous); perianth absent or comprising 1 or 2 series of smooth or barbed bristles, at maturity shorter to several times longer than mature achene. Stamens (1, 2, or) 3; filaments ribbonlike or capillary; anthers broadly ellipsoid to linear, basifixed; pollen maturing as cryptotetrads (pseudomonads), subspheroidal, trinucleate (binucleate?) when shed. Gynoecium tricarpellate and stigmas 3, or bicarpellate (dorsiventrally or laterally compressed) and stigmas 2; styles and stigmas capillary, glabrous or glandular-pubescent; ovules basal, anatropous, bitegmic, crassinucellar; megagametophyte (embryo sac) of the Polygonum type. Achene trigonous or lenticular, ovoid, obovoid, or ellipsoid, smooth, puncticulate, or papillose; endosperm mealy, with starch grains, protein crystals, and oil droplets, filling most of the achene; embryo small; embryogeny of the Onagrad (*Juncus* variation) or Asterad type; germination epigeal. Base chromosome numbers 5, 6, 7, 8. TYPE GENUS: *Cyperus* Linnaeus.

A large family of about 80 genera and 3500 species, worldwide in distribution. Seventeen genera occur in our area, including *Carex* L., with 165 species, the largest genus of seed plants in the Southeast.

There is general agreement that the Juncaceae are the closest relatives of the Cyperaceae (Thorne; Dahlgren & Rasmussen). Both families have tristichous phyllotaxy, simultaneous microsporogenesis, post-reductional meiosis, non-localized (diffuse) centromeres, anatropous ovules, and Onagrad embryogeny. The Cyperaceae are distinguished from the Juncaceae in having conical silica bodies in the epidermal cells, solitary ovules and basal placentation, pollen-grain formation in which three of the meiotic products degenerate, nuclear endosperm, and indehiscent fruits (achenes). North American Cyperaceae lack a perianth or have one of bristles; North American Juncaceae have expanded chartaceous tepals. This is useful regionally for distinguishing the two families, but it cannot be used on a worldwide basis because *Oreobolus* R. Br. and several other genera of Southern Hemisphere Cyperaceae also have chartaceous tepals.

Some authors (e.g., Fernald, Cronquist) have treated the Gramineae as the closest relatives of the Cyperaceae. However, the grasses have apical placentation, orthotropous ovules, distichous phyllotaxy, and open leaf sheaths, and their affinities are with the Restionaceae and the Flagellariaceae (Thorne; Dahlgren & Rasmussen). Also, the grasses are chemically unlike the sedges (Har-

borne, 1971). For example, anthocyanins are common in grasses but unknown in sedges, while aurones are common in sedges and unknown in grasses (and in the Juncaceae).

The tribal classification was first elaborated on a worldwide basis by Nees von Esenbeck and Kunth and has been rather stable since. Some authors recognized tribes only; some, subfamilies and tribes; and others, subtribes also. Two subfamilies, both distributed worldwide, are accepted in this treatment: the Cyperoideae (Scirpoideae Pax, flowers perfect) and the Caricoideae Pax (flowers imperfect). Included in the Cyperoideae are four tribes, of which the Scirpeae Dumort. (including Fimbristylideae Raynal; spikelets with 1 or 2 sterile basal scales, numerous fertile scales spirally arranged, perianth bristles generally present, embryos well differentiated), the Cypereae (1 or 2 sterile basal scales, several to many fertile scales distichously arranged, perianth absent, embryos well differentiated), and the Schoeneae Dumort. (Rhynchosporeae Fenzl; spikelets with several sterile basal scales, fertile scales 1 or 2 (to several), perianth bristles generally present, embryos slightly differentiated) are represented in our area. No members of tribe Hypolytreae Fenzl (Mapanieae Koyama) of the tropics grow in North America. Subfamily Caricoideae is divided into two tribes: the Scleriae Fenzl (achenes naked, borne on a hardened disk), represented in North America by a single genus, *Scleria* Berg.; and the Cariceae Dumort. (achenes enclosed in a perigynium), represented in the Southeast by *Cymophyllus* Mack. and *Carex* (and also in North America by *Kobresia* Willd., a circumboreal genus occurring in the northern United States and Canada, and *Uncinia* Pers., an austral genus extending north to Jamaica and Mexico).

Microsporogenesis in sedges differs markedly from that in other angiosperms. The nucleus of the microsporocyte divides meiotically, but cytokinesis does not follow immediately. Rather, three nuclei migrate to one end of the pollen mother cell, where they begin to disintegrate. The fourth nucleus remains in the center of the cell, where it divides mitotically. One of the resulting daughter nuclei migrates to the end of the cell, joining the other three disintegrating products of meiosis. The remaining haploid daughter nucleus divides mitotically, forming generative and tube nuclei. The generative nucleus divides again as the exine matures, resulting in the trinucleate pollen grain characteristic of the family. The four degenerated nuclei often remain visible as dark streaks near the exine. The wall of the mature pollen grain is thus homologous to the wall of the pollen mother cell. This pattern of microsporogenesis, presumably characteristic of the entire family, has been reported in *Abildgaardia* Vahl, *Bulbostylis* Kunth, *Carex, Cladium* P. Br., *Eleocharis* R. Br., *Fimbristylis* Vahl, *Fuirena* Rottb., *Scirpus* L., *Scleria,* and *Rhynchospora* Vahl. In the closely related Juncaceae cytokinesis is delayed in the pollen mother cells until each daughter nucleus has divided a second time. Thus, the Juncaceae provide a pattern of microsporogenesis intermediate to that in the Cyperaceae and other monocots, and emphasizing the relationship of the Cyperaceae and the Juncaceae.

Embryology is nearly uniform in the Cyperaceae. Endosperm formation is nuclear in all genera that have been investigated. Endosperm wall formation

is complete in most genera, but incomplete in *Rhynchospora* and *Scleria*. The mature embryos of the Cyperaceae vary considerably in shape and in the position of the cotyledon and the radicle. As a rule, each genus has its characteristic type of embryo (Van der Veken). When the achenes mature, the embryos of tribe Schoeneae are considerably less differentiated than those of other tribes (Vanhecke).

The sedges are incompletely investigated chemically, although *Cyperus* is much better known than other genera. Ethereal oils occur in the roots of three species of *Cyperus* (Hegnauer). Cyanogenesis is evidently uncommon but has been reported for three species of *Cyperus* and for one each of *Fimbristylis* and *Kyllinga* Rottb. (Gibbs). This is surprising because it is widespread in the closely related Juncaceae. Tannins occur in many sedges, having been reported in *Cyperus, Dulichium* Pers., *Fuirena,* and *Scirpus* (one species each). Alkaloids are rare; brevicarine, brevicolline, and harman occur in *Carex brevicollis* DC. (Gibbs). Some terpenoids have been reported. Citral, a monoterpenoid, occurs in species of *Kyllinga* (Gibbs), and several sesquiterpinoids are known from species of *Cyperus* (Hegnauer). Quinones are found in both *Cyperus* and *Fimbristylis* (Allan *et al.*). Leucoanthocyanins are reported from species of *Carex, Cyperus, Dulichium, Kyllinga,* and *Scirpus*. Anthocyanins are absent from the family (Harborne; Harborne *et al.*).

Flavonoids occur in many genera (Kukkonen, 1969; Harborne). Recently, Harborne and collaborators have done much to expand what is known about flavonoids in sedges. Among this class of compounds are aurones, which give a yellowish tint to the inflorescences of many sedges. These are absent from the Gramineae and the Juncaceae. Flavonols were present in only 15 percent of 11 genera tested by Harborne. Flavonoid aglycones, especially quercetin and luteolin, are widespread in the family, as are proanthocyanidins (particularly in the leaves). Harborne and colleagues (p. 765) concluded that there are "no dramatic correlations between flavonoid distribution and higher level classification of the Cyperaceae." However, certain genera or subgenera are distinguished chemically from closely related groups (see under *Cyperus* and *Abildgaardia*). Flavonoid profiles have been shown to distinguish between related taxa in *Carex* and *Cyperus* (discussed under those genera).

Metcalfe presented much useful information on the anatomy of the Cyperaceae, including clear illustrations and insightful comments on the taxonomic significance of anatomical features. Many of his descriptions were derived from studies of specimens collected in the Southeast, particularly Florida.

Developmental anatomy and morphology have received some attention (Barnard). The apex of spikelets in all examples studied conforms to the tunica-corpus pattern. Periclinal division of dermatogen and hypodermal cells gives rise to tissues that develop into the scales subtending flowers (*Scirpus, Cyperus*), the carpels (in all species), the perianth bristles (*Scirpus*), and the perigynia (*Carex*).

The first fossil remains of the Cyperaceae date from the Eocene. Fruits of *Carex, Scleria,* and *Scirpus* are known from the Eocene and Oligocene of Eurasia and North America; those of *Dulichium* and *Cladium* from the Oli-

gocene and Pliocene of Europe. Reports of Cyperaceae from pre-Tertiary strata (i.e., *Caricopsis* Samylina) are not considered reliable (Daghlian).

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KEY TO THE GENERA OF CYPERACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *perennial* (*occasionally annual*), *often rhizomatous herbs of diverse, usually wet, often disturbed habitats; rhizomes frequently present; leaves linear, the sheaths usually closed; inflorescences simple or variously branched, lateral or crowded at the apices of the culms; flowers perfect or imperfect* (*the plants very rarely dioecious*), *borne in the axils of scales or in perigynia; perianth bristles present or absent; fruit an achene; embryo small; endosperm abundant.*

A. Flowers perfect (staminate or carpellate flowers infrequently formed at base or apex of spikelets).
  B. Scales of the spikelets spirally arranged.
    C. Achenes without obconical or pyramidal apical tubercle, but sometimes with persistent swollen style base much less than half as wide as the achene.
      D. Achenes subtended by 15–20 cinnamon or whitish, silky bristles 5–10 times as long as the achenes. . . . . 2. *Eriophorum.*
      D. Achenes subtended by bristles at most 3 times as long as the achenes, or with bristles lacking.
        E. Inner whorl of perianth bristles with expanded spongy petaloid blades. . . . . 3. *Fuirena.*
        E. Perianth bristles absent or lacking expanded blades.
          F. Bulbous base of style persistent on mature achenes. . . . . 6. *Bulbostylis.*
          F. Base of style not persistent.
            G. Styles fimbriate. . . . . 5. *Fimbristylis.*
            G. Styles smooth.
              H. Spikelets maturing a single achene; bristles absent. . . . . 14. *Cladium.*
              H. Spikelets maturing several to many achenes; bristles usually present.
                I. Spikes and spikelets borne on rays, rarely sessile; achenes and scales appressed to rachilla. . . 1. *Scirpus.*
                I. Spikelets sessile; achenes and scales borne at right angles to rachis. . . . . 10. *Lipocarpha.*
    C. Achenes with pyramidal or obconical apical tubercle ½ to nearly as broad as the achene.
      J. Leaf blades absent; inflorescences unbranched, a single spikelet terminating the culm. . . . . 4. *Eleocharis.*
      J. Leaf blades present; inflorescence of several to many spikelets, some usually borne on branches. . . . . 11. *Rhynchospora.*
  B. Scales of the spikelets distichously arranged.
    K. Perianth bristles absent.
      L. Plants bulbous-thickened basally; style base sclerified, persistent; spikelets 1(–3). . . . . 7. *Abildgaardia.*
      L. Plants not bulbous-thickened basally; style base soft, deciduous; spikelets numerous.
        M. Inflorescences branched; spikelets 1- to many-flowered; rachilla elongate; scales broadly rounded. . . . . 8. *Cyperus.*
        M. Inflorescences unbranched (spikes sessile); spikelets 1- (infrequently 2-)flowered; rachilla not or barely elongate; scales conduplicate, conspicuously keeled. . . . . 9. *Kyllinga.*
    K. Perianth bristles present.
      N. Leaves cauline; inflorescences several, axillary. . . . . 12. *Dulichium.*
      N. Leaves basal; inflorescence solitary, terminal. . . . . 13. *Schoenus.*

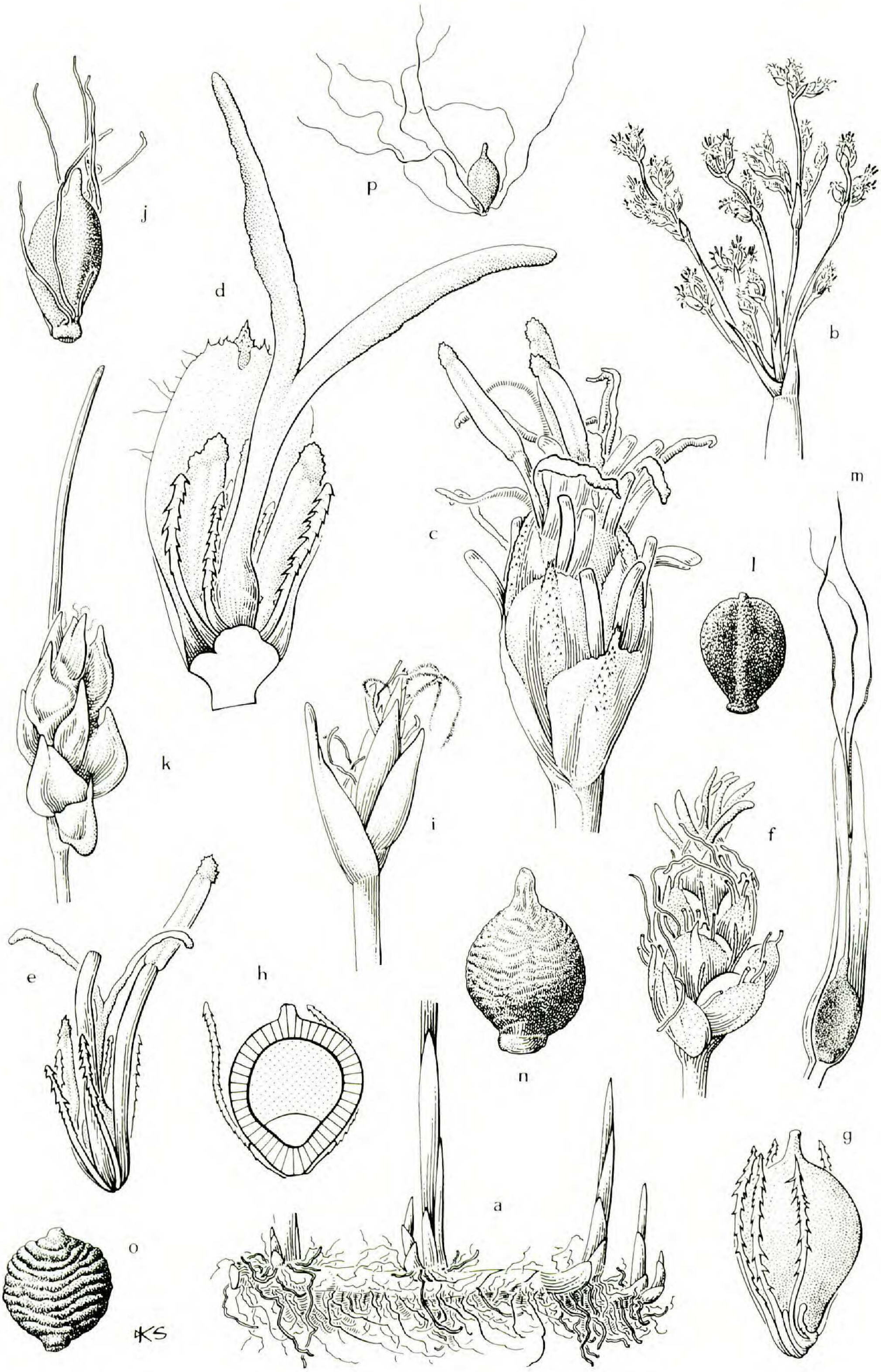
A. Flowers strictly imperfect.
  O. Achenes naked, often borne on a discoid hypogynium. ..... 15. *Scleria.*
  O. Achenes enclosed in perigynia.
    P. Spikes single, white; leaf blades broadly lanceolate, the apices broadly rounded, the midvein not distinguishable from other veins. .. 16. *Cymophyllus.*
    P. Spikes 1 to several, greenish, yellowish green, or light brown; leaf blades linear, the apices acute, the midvein much larger and more conspicuous than other veins. ..... 17. *Carex.*

Subfamily CYPEROIDEAE

Tribe SCIRPEAE Kunth ex Dumortier, Fl. Belg. 143. 1827.

1. **Scirpus** Linnaeus, Sp. Pl. **1:** 47. 1753; Gen. Pl. ed. 5. 26. 1754.

Small to medium-sized perennials or annuals of shallow fresh or tidal waters, disturbed moist soils, moist [mesic to dry-mesic] woodlands, marshes, open mountaintops, and grassy balds. Roots fibrous; perennial species with rhizomes short, branched, producing loose to dense tussocks of culms; annual species without rhizomes, forming dense clumps of culms. Culms trigonous (with planar, concave, or slightly convex surfaces) or terete, smooth throughout or scabrellate distally. Leaves all basal or scattered along the culm; sheaths closed, smooth or sometimes with conspicuous cross veins, greenish white, reddish brown, or blackish; blades flat, conduplicate, or subterete, ½ to nearly as long as the culm, stiff or arching (limp when growing underwater); stomata paracytic; chlorenchyma not radiate; longitudinal air chambers often present. Involucral leaves (1 or) 2–10, the blades resembling cauline ones but sheaths generally much shorter, approximate at the summit of the culm or rather widely spaced over the upper ⅓ of it, horizontal to ascendent, or the longest nearly vertical and simulating a continuation of the culm. Inflorescences composed of primary and secondary (sometimes tertiary) rays, in many species reduced to glomerulate clusters or heads, in some to a cluster of several more or less sessile spikelets or a single sessile spikelet; prophylls of the rays tubular, obtuse to acute apically, smooth but usually conspicuously costate; primary rays smooth, or scabrellate distally or throughout, terete, stiff or flexuous, secondary (and sometimes tertiary) rays similar to primary ones, but shorter and usually more slender. Spikelets ovoid to linear-oblong. Scales (3 to) 20 to about 100, spirally arranged and closely imbricate, with 2 lowermost sterile and others fertile, all deciduous at maturity, ovate to oblong, with 1–9 subtle to conspicuous nerves and sometimes a conspicuous midrib, the apex obtuse to acute, entire or mucronulate to strongly cuspidate, the awn straight to strongly excurved. Flowers perfect, protogynous. Perianth bristles 3–6(–8) or lacking, smooth or retrorsely scabrellate, straight, highly curled, or crinkled at maturity, from ⅓ to 4 times as long as the mature achene, deciduous or remaining attached to the mature achene. Stamens (2 or) 3; filaments slender, about equaling the subtending scales; anthers broadly ellipsoid to narrowly linear, the apices of the connectives in some species prolonged as subulate appendages up to ¼ the length of the anther, sometimes tipped with crystalline prickles; pollen uniaperturate, subspheroidal in polar view and triangular to obovoid in equatorial view, psilate,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bi- or trinucleate. Styles capillary; stigmas 2 or 3, about equaling the style in length. Achenes lenticular to trigonous, equilateral in transverse section, or slightly to strongly dorsiventrally flattened, the base stipitate or cuneate, the apex apiculate, beaked, or entire, the surface essentially smooth, finely pitted, reticulate, or rugulose. Embryos ellipsoid, turbinate, or fungiform, the radicle lateral or basal. Base chromosome numbers 5, 7. LECTOTYPE SPECIES: *Scirpus sylvaticus* L.; see Hitchcock & Green, Prop. Brit. Bot. 118. 1929. (Latin name for a bulrush, probably *Scirpus Tabernaemontani* Gmelin.)—BULRUSH, REED, CLUB-RUSH, WOOL-GRASS, THREE-SQUARE.

Scirpus, the third-largest genus of the Cyperaceae, with about 300 species worldwide, is best represented in temperate regions. North America (including Mexico), with about 80 species, is the center of diversity. Only about 15 species occur in the West Indies and Central America, and about 30 in all of South America, most of these in Argentina and Chile. Twelve species occur in Europe, and perhaps 50 in Africa. It is difficult to estimate the number of species in all of Asia; 24 grow in the Soviet Union, and ten in Malesia. A recent synopsis included 44 in Australia (Wilson).

Studies in *Scirpus* have been hampered by lack of a worldwide treatment (such as those prepared for several other large genera of the family, i.e., *Carex, Cyperus, Eleocharis,* and *Rhynchospora*). Some botanists (e.g., Wilson, Koyama) have recognized each of the sections at the generic level. Most American authors (Fernald, Schuyler), however, have recognized the genus in a broad sense; this traditional circumscription is accepted here. Although several researchers have lamented the "diverse" nature of the genus, most of the kinds of variation that are represented in *Scirpus* are also present in *Cyperus,* which

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FIGURE 1. *Scirpus* sect. JUNCO-SCIRPUS. a–h, *S. Tabernaemontani* (*S. validus*): a, underwater rhizome collected late in season, apex at right (note remains of shoot of current season and developing shoots of next year's growth), × ½; b, apex of culm with inflorescence, × 1; c, single spikelet with lower flowers past anthesis (filaments visible), upper ones with anthers visible and styles exserted, × 12; d, flower and subtending scale removed from spikelet, view of adaxial surface, stigmas exserted, anthers still included (note barbed bristles), × 20; e, flower, showing different maturation of stamens, the stamen to right with elongate filament and anther ready to dehisce, the middle stamen with anther fallen, the stamen to left before elongation of filament, × 12; f, spikelet at stage later than that in "c," immature achenes below and flowers with receptive stigmas above, × 6; g, mature achene with persistent bristles, × 12; h, same, in vertical section, fruit wall hatched, endosperm stippled, embryo unshaded (seed coat too thin to show), × 12. i, j, *S. cespitosus:* i, spikelet, lower flowers with persistent filaments, upper ones with exserted stigmas, involucral bracts greatly reduced, scalelike, spikelet solitary, × 6; j, achene with smooth bristles, × 12. k, l, *S. koilolepis:* k, solitary spikelet, subtended by scalelike involucre, scales keeled, × 6; l, mature, trigonous, bristleless achene, × 12. m–o, *S. Erismaniae:* m, basal flower in axil of leaf, × 6; n, achene from basal flower, × 12; o, achene from cauline spikelet, × 12. p, *S. cyperinus:* achene with elongate bristles, × 12.

has traditionally been maintained as one genus. Moreover, there has yet to appear a thorough study of *Scirpus* that presents compelling arguments for recognizing *Schoenoplectus* (Reichenb.) Palla, *Trichophorum* Pers., *Baeothryon* A. Dietr., and other segregate genera. Many useful papers on the taxonomy of single species or groups of species have been written by several authors, most notably Schuyler.

The achenes of species of *Scirpus* are probably dispersed after being eaten by waterfowl (McAtee) (wild ducks in the case of *S. paludosus* Nelson). Most are digested, but those that survive have 94 percent germination, compared with two or three percent for those treated with acid or alkali, and nine percent after fermentation treatment (Low). Light is required for germination (Isely). Achenes of many species, particularly *S. cyperinus* (L.) Kunth, are probably dispersed by the wind, although their long, contorted perianth bristles likely also cause them to cling to fur or feathers.

Some 30 species of *Scirpus*, representing six sections, occur in our area. Following is a brief account of these.

Species with leafy stems are classified in three sections. In all of these, leaves are borne along the length of the culm, while in plants of other sections they are basal. Schuyler (1961, 1962, 1963, 1964, 1966, 1967a, 1967b, 1967c, 1971b) has studied the species with leafy stems and has provided most of the available information on morphological variation, cytology, hybridization, and distribution.

Section SCIRPUS (sect. *Taphrogeton* (Reichenb.) Ascherson; plants leafy stemmed; spikelets in dense heads; achenes ellipsoid, with perianth bristles straight, about as long as the achenes) includes the type species, the Eurasian *Scirpus sylvaticus* L., $n = 31, 32$. The section is represented by seven species in our area, which fall into three groups. The first includes the North American relatives of *S. sylvaticus*, among which the only representative occurring in the Southeast is *S. expansus* Fern., $n = 32$. This bulrush grows mostly in the Northeast, but it ranges south in the Appalachians to northern Georgia and northern Alabama. A second eastern North American species, *S. microcarpus* Presl (*S. rubrotinctus* Fern.), $n = 33$, occurs southward to the uplands of West Virginia and also in western North America and eastern Asia.

The second group (leaves tristichous, spikelets in glomerules, plants typically viviparous, bristles straight) includes what was treated as *Scirpus atrovirens* Willd. by Fernald (1950). Schuyler (1967a, 1967b, 1967c) demonstrated that there are four species in this group that can be distinguished morphologically and separated geographically and phenologically. *Scirpus georgianus* Harper, $n = 25, 26, 27$, is the most common in our area (specimens examined from every state). It lacks a perianth and leaf cross veins (these are present in the more northern *S. atrovirens* Willd., $n = 28$, which is occasional in our area from the Ridge and Valley Province westward). *Scirpus Hattorianus* Makino, $n = 28$, is a northeastern species known in our area from only six collections from the uplands of North Carolina, Tennessee, and Alabama. *Scirpus flaci-difolius* (Fern.) Schuyler, $n = 27$, is endemic to river bottoms in eastern Virginia and northeastern North Carolina.

The third group of sect. SCIRPUS (leaves distichous, spikelets in glomerules,

plants not viviparous, bristles contorted) is represented by a single species in North America, *Scirpus polyphyllus* Vahl, $n = 29$, which is known from all the Southeastern States.

Section ANDROCOMA (Nees) Bentham (plants leafy stemmed; perianth bristles smooth, approximately as long as the subtending scales) is represented in our area by three species. *Scirpus pendulinus* Muhl. (*S. lineatus* auct., non Michx.), $n = 20$, has the greatest range of the three, occurring from Maine to Minnesota south to the Gulf Coast. *Scirpus lineatus* Michx. (*S. fontinalis* Harper), $n = 18$, is found along the Coastal Plain from Virginia to Florida; *S. divaricatus* Ell., $n = 14$, has a similar range but is found westward to Louisiana.

Section TRICHOPHORUM (Pers.) Darl., the wool grasses (plants leafy stemmed; perianth bristles contorted, several times longer than the achenes), comprises several species of cold-temperate regions. At maturity the elongate, crinkled bristles give the spikelets and the inflorescences a woolly appearance. Extensive hybridization in this group has resulted in a nomenclatural mire of species, varieties, and forms. Schuyler (1962, 1967a) has carefully documented infraspecific variation, cytology, and hybridization; he concluded that only a single species, *Scirpus cyperinus* (L.) Kunth (including *S. rubricosus* and *S. eriophorum* Michx.), $n = 33$, should be recognized in the Southeast. Three others that hybridize with *S. cyperinus*, *S. pedicellatus* Fern., $n = 34$; *S. Longii* Fern.,[3] $n = 33$; and *S. atrocinctus* Fern., $n = 34$, occur in the Northeast.

Section OXYCARYUM (Nees) Beetle (plants rhizomatous; heads of spikelets ovoid, pedunculate; scales acute, excurved) is represented in the Southeast by a single species, *Scirpus cubensis* Poeppig & Kunth. In our area the species occurs from southern Florida to Louisiana in brackish or freshwater marshes. The affinities of this section are unclear, and no chromosome counts are available.

Section BOLBOSCHOENUS (Ascherson) Beetle (plants tall; spikelets large, few; scales awned, pubescent) is represented in our area by two species of freshwater or tidal wetlands. *Scirpus robustus* Pursh grows in tidal marshes and estuaries from eastern Canada to Texas. A second species, *S. cylindricus* (Torr.) Britton, occurs in marshes from Delaware to Georgia. It was confused with *S. robustus* and *S. etuberculatus* until it was restudied by Schuyler (1975). The third species, *S. etuberculatus* (Steudel) Kuntze, grows in brackish waters and is known near the coast from Delaware to Louisiana. It is morphologically transitional to the next section (Fernald, 1950).

Section JUNCO-SCIRPUS Syme[4] (sect. *Pterolepis* Beurl., sect. *Schoenoplectus* (Reichenb.) Bentham) (plants tall; culms often leafless; involucral leaves 1 or 2, more or less erect; achenes sessile, beaked, with bristles persistent) is represented in the Southeast by seven species. *Scirpus pungens* Vahl (*S. americanus*

[3]Reported from North Carolina by Cappel and Radford and colleagues. I was unable to locate any specimens to substantiate this. According to Schuyler (1962; pers. comm.), records of *S. Longii* from south of New Jersey were the result of misidentifications of *S. cyperinus*.

[4]*Scirpus* sect. JUNCO-SCIRPUS Syme in Sowerby, Engl. Bot. ed. 3. **10:** 62. 1870. LECTOTYPE SPECIES (here designated): *S. lacustris* L. Syme included three species in this section, *S. lacustris*, *S. triqueter* L., and *S. pungens* Vahl; *S. lacustris* is the only one with terete culms suggesting those of plants of the genus *Juncus* L., a feature emphasized by the sectional name.

auct., non Pursh), $n = 39$, of sunny wetlands, is widespread in temperate North America and occurs in all the southeastern states. It is closely related to *S. americanus* Pursh (*S. Olneyi* Gray), $n = 39$, a taller, thicker-stemmed species of tidal, alkaline, or saline marshes from Massachusetts to Florida and west to southern California. The two species occasionally hybridize in brackish upper edges of tidal marshes, but in general they are isolated ecologically. A recently described species, *S. deltarum* Schuyler, $n = 39$, occurs in the Mississippi Delta region, the Mobile Bay area, and disjunctly in the prairie marshes of eastern Kansas and Missouri. A fourth species, *S. subterminalis* Torrey, $n = 37$, is widespread in eastern North America but is known in the Southeast from only a few collections from the Coastal Plain and Piedmont of North and South Carolina. Two growth forms exist: submersed, in which the leaves are filiform and flaccid, and terrestrial or stranded, in which they are conduplicate and stiff (Schuyler, 1972b). The highly reduced inflorescence consists of a single spikelet subtended by one erect involucral bract. The species has an unusual photosynthetic metabolism: the tissues of the stem, leaf, and rhizome accumulate malic acid at night, providing a reservoir of fixed carbon for photosynthetic reactions during daylight (Beer & Wetzel). Such physiology is similar to that of terrestrial plants having crassulacean-acid metabolism.

The remaining three species of sect. JUNCO-SCIRPUS were once segregated as sect. *Pterolepis* (Fernald, 1950). These reportedly differ in having plumose bristles and pedunculate clusters of spikelets. However, on a worldwide basis several extraregional species are intermediate with respect to these two characters; Koyama (1963) therefore concluded that the two sections should be merged. *Scirpus Tabernaemontani* Gmelin (*S. validus* Vahl), $n = 21$, grows in freshwater marshes nearly throughout the United States and southern Canada and in much of the Old World; it is common throughout the Southeast. *Scirpus acutus* Bigelow, $n = 19$, a species of the Midwest and Great Plains, is represented in our area by a few collections from North Carolina and Tennessee. Dabbs studied these two species in Saskatchewan and found that they were morphologically distinct. Hybrids were occasionally found, but these were sterile and spread only by rhizomes. A western species, *S. californicus* (C. Meyer) Steudel, $n = 34$, is known from a few places in Louisiana, Mississippi, and South Carolina. Other North American species of *Scirpus* lack its plumose perianth bristles. *Scirpus heterochaetus* Chase, $n = 19$, might be found in the northwestern part of our area; it is a species of quiet calcareous waters of the St. Lawrence and upper Mississippi drainages.

Section BAEOTHRYON Dumort.[5] (plants caespitose, often forming tussocks; leaves basal; inflorescences of a single terminal spikelet; involucral bract greatly reduced, resembling a fertile scale of the spikelet) is represented by four species in northeastern North America. Only one of these, the circumboreal *Scirpus cespitosus* L., reaches our area, growing in the grassy balds of the high mountains of North Carolina, Georgia, and Tennessee. The southeastern populations are disjunct from the nearest occurrences of the species in the northeastern United

[5] *Scirpus* sect. BAEOTHRYON Dumort. Fl. Belg. 143. 1827. Fernald (1947, 1950) and other authors have attributed the sectional name to Endlicher (Gen. Pl. 118. 1836).

States (in the Adirondack Mountains of New York) by some 1200 km. A widespread but easily overlooked species of the northeastern and midwestern United States, *S. verecundus* Fern., has not yet been collected in our area but might occur in the uplands of North Carolina, Tennessee, or Arkansas. It is perhaps the most mesic species of the genus in North America, inhabiting dry woodlands and basic ledges, in contrast to the aquatic habitats of most species of *Scirpus*.

Section Isolepis (R. Br.) Griseb. (plants annual; inflorescences unbranched; spikelets sessile, few) is represented in our area by five species. *Scirpus koilolepis* (Steudel) Gleason probably occurs in all the states in our area, as well as in the Midwest and the Great Plains. The remaining species are much less frequent and are local in range. *Scirpus Erismaniae* Schuyler, $n = 5$, is recorded from Georgia, western Florida, and Alabama. This species produces basal spikelets on very short culms (see Figure 1), as do several African species of this section (Haines). *Scirpus molestus* M. C. Johnston, described from Texas, also occurs in southern Louisiana. The remaining species have perianth bristles (in most collections) and have been distinguished by some authors (e.g., Fernald, 1950) as sect. *Actaeogeton* (Reichenb.) Beetle. *Scirpus Hallii* Gray, $n = 11$, known from widespread localities in the eastern United States, has been collected in Georgia; and *S. Purshianus* Fern., $n = 19$, a primarily northeastern species, is known in the Southeast from North and South Carolina, Tennessee, and Georgia.

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2. **Eriophorum** Linnaeus, Sp. Pl. **1:** 52. 1753; Gen. Pl. 27. 1754.

Small to medium-sized, single-stemmed or loosely caespitose [densely caespitose or tussock-forming] perennials of bogs, swamps, and pocosins. Roots fibrous; rhizomes short, horizontal to oblique. Culms terete or nearly so, glabrous. Leaves basal and cauline; sheaths glabrous, ligules lacking; blades flat [conduplicate], the midrib conspicuous, the margins scabrellate, especially distally; chlorenchyma not radiate; air chambers present. Inflorescences of 1 to several sessile or pedunculate spikelets; bracts 1–6, closely spaced at the summit of the culm, oblique or slightly reflexed [ascendent to erect], sheaths very short, blades leaflike; rays short [elongate and drooping or absent]. Spikelets oblong-ovoid; empty basal scales 3–5[–15]. Scales 50–150, oblong-ellipsoid, acute to obtuse, 1- to 5-nerved, deciduous after the achenes mature. Flowers perfect. Perianth bristles [6 to] 12 to ca. 50, about equaling the scales at anthesis but elongating greatly as the achenes mature. Stamens 1 [or 2 or 3]; filaments flattened; anthers linear [ellipsoid], the apices of the connectives not prolonged. Styles capillary, glabrous; stigmas 3, about as long as the style. Achenes trigonous, slightly compressed dorsiventrally, oblong-ellipsoid (widest in distal half), the apex obtuse, apiculate, the base sessile, the surface smooth, glossy. Embryos more or less turbinate [obconical or ellipsoid], the radicle sublateral. Base chromosome number 29. TYPE SPECIES: *E. vaginatum* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 322. 1913. (Name from Greek, *erios,* cotton or wool, and *phoros,* bearing, in reference to the cottony mature inflorescence.)—COTTON-GRASS, BOG-COTTON.

A genus of about 12 species of boreal regions. About eight species are circumpolar, occurring in both northern Eurasia and northern North America. There is relatively little endemism. Only *Eriophorum virginicum* L. occurs in the Southeast; it ranges from Newfoundland to Minnesota southward and is known in our area from a few scattered collections made in the mountain bogs of North Carolina and Tennessee and the Coastal Plain swamps of North Carolina, South Carolina, and Georgia (southern limit in the Okefenokee Swamp). No species of the genus is reported from Missouri or Kentucky, and only *E. virginicum* occurs in Virginia and West Virginia.

A few workers (e.g., Koyama) have treated the cotton grasses as constituting *Scirpus* sect. *Vaginati* (Andersson) Koyama, but most have kept *Eriophorum* separate from *Scirpus.* The two genera are readily distinguished by the number and the length of the perianth bristles. *Eriophorum* is divided into two sections (Goncharov *et al.*), each with about six species: sect. ERIOPHORUM (sect. *Vaginati* Andersson) contains those species in which the inflorescence is a single sessile spike, while sect. PHYLLANTHELA Andersson comprises those (including *E. virginicum*) in which the inflorescence consists of several pedunculate spikes.

The genus is almost uniform cytologically; ten of the 12 species have been counted as $n = 29$. Two are $n = 27$, and in the case of *Eriophorum angustifolium* L., $n = 29$ and $n = 35$ have been reported.

Hybridization is known among both the Eurasian and the North American species. Although it is generally not difficult to distinguish *Eriophorum virginicum* from the other members of the genus, there are species pairs that appear to intergrade—for example, *E. angustifolium* and *E. viridicarinatum* (Engelm.) Fern. It is surprising that the genus has not received more systematic study, considering its broad distribution.

The circumboreal *Eriophorum alpinum* L., $n = 29$, was placed in *Scirpus* (as *S. hudsonianus*) by Fernald. Following a survey of epidermal features of achenes of *Scirpus* and *Eriophorum,* Schuyler concluded that the species belongs in *Eriophorum.* Its chromosome number also supports this placement.

In the Arctic, species of *Eriophorum* are dominant and sometimes form a vegetation type known as "tussock tundra." The plants provide an important forage for deer and caribou in North America and for sheep, ponies, and reindeer in northern Europe and Asia. In the United States the plants are seldom dominant (except in alpine grasslands in limited montane areas). However, they sometimes form a conspicuous element of fen and bog vegetation because of their showy fruiting heads.

Wein summarized ecological information about *Eriophorum vaginatum,* a circumboreal tussock-forming species. Species of *Eriophorum* occurring in the eastern United States are rhizomatous or rather loosely caespitose. There is much information on the autecology and physiological ecology of the genus, although nearly all is derived from studies of *E. vaginatum.*

Despite its abundance in arctic regions, *Eriophorum* has conspicuously few insect herbivores. Larvae of the cottongrass moth, *Celaena haworthi* Curtis, tunnel in the culms of *E. vaginatum* in Europe, but no macrolepidopteran species is reported to feed on *Eriophorum* species in North America (Tietz). The aphid *Rhopalosiphum eriophori* (Walker) is reported on *E. angustifolium* and *E. vaginatum.* The larvae of the beetle *Plateumaris discolor* (Panzer) live in anaerobic conditions among the roots of *E. vaginatum* in Europe, obtaining needed oxygen by tapping into the intercellular air spaces in the cortex of the roots.

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3. **Fuirena** Rottboell, Descr. Icon. 70. 1772.

Rhizomatous perennials or caespitose annuals of sunny, wet, often disturbed soils. Rhizomes horizontal, covered with persistent lanceolate scales, producing cormlike axillary offshoots from which new culms arise. Culms erect or slightly inclined, unbranched, terete, hollow. Leaves with sheaths tubular, costate, pubescent, barely reaching to decidedly separated from the base of the next sheath, the ligules hyaline, hispid (or glabrous) apically; basal leaves bladeless, cauline leaves with blades lanceolate to linear, flat or slightly conduplicate [crescentiform], pubescent (blades absent or reduced to an awned apex of the sheath in 1 species); stomata paracytic; chlorenchyma not radiate. Inflorescences of 1 to several sessile or pedunculate glomerules in the axils of the upper leaves; rays lacking or 1–4, smooth or hispidulous. Spikelets 1–6, ovoid to oblong. Scales 30–60(–100 or more), ovate to oblong, widest at or above the middle, hispid adaxially, less often glabrous or glabrescent, 3- to 9-nerved, the 3 central nerves prolonged into a cuspidate, straight, or excurved apex ⅕ as long as to nearly equaling the length of the body of the scale, the 3 basal scales sterile, longer, narrower, and more conspicuously awned than the fertile ones. Flowers perfect, protogynous. Perianth biseriate [uniseriate or absent], outer whorl (sepals) of 3 smooth or retrorsely scabrellate bristles, ¼ to nearly as long as the achene; inner whorl (petals) of bristles bearing expanded, entire [fimbriate], hyaline to somewhat spongy blades with obtuse, acute, aristate, or emarginate apices. Stamens 3 (infrequently 1, 2, or 6); filaments ribbonlike, about as long as the subtending scale; anthers linear to ellipsoid; pollen grains uniaperturate, obovoid to subspheroidal, psilate, trinucleate. Styles linear, frequently hispid; stigmas 3, linear, about as long as the styles, pubescent. Achenes trigonous with conspicuous ridged angles, ellipsoid, the apex acute but not apiculate, the base stipitate (usually conspicuously so), the faces flat to slightly concave, delicately striate or smooth [cancellate], glossy. Embryo fungiform. Base chromosome number 23. (Including *Vaginaria* Persoon.) LECTOTYPE SPECIES: *F. umbellata* Rottb.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 337. 1913. (Named for Joergen Fuiren, 1581–1628, Danish physician.)

A warm-temperate and tropical genus of about 30 species. Seven occur in the Southeast; these are well known through Kral's recent revision. An additional three occur in the southwestern United States. *Fuirena repens* Boeck. is endemic to Mexico, while five primarily South American species extend northward into Central America, Mexico, and the West Indies. About 12 species occur in South America, and about as many in Africa. Only *F. umbellata* is recorded in Europe, and it is limited to the southern part of the continent. Five species occur in southern Asia, but none is recorded from the Soviet Union.

Most of our species are distributed from Texas to Florida along the Gulf Coastal Plain and northward on the Atlantic Coastal Plain. *Fuirena scirpoidea* Michx. and *F. longa* Chapman occur only as far north as southern Georgia, *F. breviseta* Cov. as far as eastern Virginia, *F. squarrosa* Torrey north to Long Island, and *F. pumila* to Cape Cod. The last species is disjunct in southern Michigan and northern Indiana. Two others in our area, *F. Bushii* Kral and *F. simplex* Vahl, are southern Great Plains species that occur eastward to Louisiana, Arkansas, and Missouri.

All of the southeastern species have haploid chromosome numbers of 23. The only exception is *Fuirena simplex,* for which $n = 15$ has been reported from Texas populations, in addition to $n = 23$ from southeastern representatives (Kral).

Plants of *Fuirena* have no reported economic significance in North America, although *F. glomerata* Lam. and *F. umbellata* have been reported as important weeds in Borneo, India, Taiwan, and Malaysia (Holm *et al.*).

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4. **Eleocharis** R. Brown, Prodr. 224. 1810.

Small to medium-sized, loosely to densely caespitose or single-stemmed, rhizomatous or stoloniferous, submersed, emergent, or littoral perennials (rarely annuals) of marshes, ditches, and pond and river shores. Roots fibrous; rhizomes (lacking in some species) slender, horizontal, covered with appressed ovate to lanceolate scales. Culms terete or ellipsoid (less often trigonous, quadrangular, or flattened), solid or hollow (sometimes with thin transverse parenchymatous septa), smooth, with numerous paracytic stomata (submersed lower portions of culms with few or no stomata); in submersed species secondary branches present, very closely spaced and seemingly verticillate. Leaves 1–4; sheaths closely fitting the base of the culm, the summit firm or scarious (sometimes apiculate); blades lacking. Inflorescences single spikelets terminating the culms. Spikelets slenderly cylindrical to ovoid, slightly less than to about 3 times thicker than the summit of the culm. Scales (2–)20–100, oblong, lanceolate, obovate, or orbiculate, hyaline, firm, or coriaceous, strongly to weakly nerved or nerveless, deciduous or persistent. Flowers perfect. Perianth bristles (3–)6(–12) or absent, extrorsely or retrorsely barbed or smooth, persistent on the base of the mature achene or falling from it. Stamens 3; filaments hyaline, about equaling to shorter than the subtending scale; anthers ellipsoid to linear; pollen grains 1- [to 4-]aperturate, obovoid to subspheroidal, psilate (scabrellate), trinucleate. Styles with swollen, bulbous base; stigmas 2 or 3, capillary. Achenes lenticular or trigonous, ovoid, obovoid, or ellipsoid, the base broadly rounded, the apex capped by a small to large, pyramidal, conical, or swollen tubercle, the surface smooth or variously reticulate, dull, frequently glossy, or iridescent. Embryos turbinate to fungiform. Base chromosome number 5. TYPE SPECIES: *E. palustris* (L.) Roemer & Schultes (*Scirpus palustris* L.); see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1**: 310. 1913. (Name from Greek, *helos,* marsh, and *charis,* grace, from the paludal habitat of most species.)—SPIKE-RUSH, DOG'S-HAIR GRASS.

A genus of about 250 species, worldwide in distribution. *Eleocharis* is evidently closely related to *Scirpus* but is distinguished by its leafless culms and its single, erect, terminal spikelets. Although the apical tubercles of the achenes of *Eleocharis* are similar to those of some species of *Fimbristylis* Vahl, suggesting that *Eleocharis* is most closely related to that genus (Svenson, 1929), recent evidence supports a closer relationship between *Scirpus* and *Eleocharis.* Both of these genera have non-kranz anatomy, while *Fimbristylis* has kranz anatomy (Metcalfe). The embryos of *Eleocharis* (turbinate to fungiform, radicle basal, coleoptile lateral) are similar to those of species in *Scirpus* sect.

BOLBOSCHOENUS (Van der Veken), rather than to those of *Fimbristylis* (turbinate to fungiform, radicle lateral, coleoptile basal).

Some 40 species occur in the Southeast, and many of these have rather wide ranges. Holarctic, neotropical, and pantropic groups are represented in our area. Svenson's (1929, 1957) division of the genus into seven series has received wide acceptance, and our species are presented here according to his classification. The two largest are ser. ELEOCHARIS (ser. *Palustriformes* Svenson) and ser. TENUISSIMAE Svenson, having 13 and ten species in our area, respectively.

Plants of ser. ELEOCHARIS are characterized by slender culms and a stoloniferous habit; there are both tristigmatic and distigmatic species. Our representatives are mostly northeastern species that occur southward only as far as Virginia, Tennessee, or Arkansas. However, *Eleocharis fallax* Weatherby, $2n = 42$, and *E. arenicola* Torrey, $2n = 20$, both of the Coastal Plain, are found in most of the Southeastern States. *Eleocharis montevidensis* Kunth, $2n = 10, 20$, is a neotropical species that has been found north to the Carolinas and California; it is sometimes treated as conspecific with *E. arenicola*.

Plants of ser. TENUISSIMAE are loosely caespitose and have slender, wiry culms. Our species are mostly restricted to the Coastal Plain. In the Southeast the neotropical *Eleocharis nana* Kunth has been found only in southern Florida, while *E. nodulosa* (Roth) Schultes occurs along the Gulf Coast from Florida to Louisiana. The most widely distributed of our species, *E. tuberculosa* (Michx.) Roemer & Schultes, $2n = 30$, is found throughout the Southeast northward to Nova Scotia. It is distinctive in having perhaps the largest tubercle in any species of the genus—as large as the body of the mature achene.

Plants of ser. MUTATAE Svenson are the tallest in the genus; three of our species regularly reach 1 m. The plants are characterized by spikelets that are barely wider than the apices of the subtending culm and that have persistent scales. The plants are unusual ecologically because they grow in ponds or pools with a stable water level. Most other species of the genus grow where receding water levels leave the plants exposed in summer. Species of ser. MUTATAE have very high chromosome numbers. Briggs has made counts for the Australian *Eleocharis equisetina* Presl, $2n = 172$, and *E. sphacelata* R. Br., $2n = 94$–100, 140, 180, 188. Six species of the series occur in our area: *E. equisetoides* (Ell.) Torrey and *E. quadrangulata* (Michx.) Roemer & Schultes are reported throughout the Southeast and range north to southern New England; *E. cellulosa* Torrey, *E. interstincta* (Vahl) Roemer & Schultes, and *E. elongata* Chapman are restricted to the Coastal Plain; and *E. Robbinsii* Torrey, a species mainly of the Northeast, ranges south to Virginia and northern Florida along the Coastal Plain. Tubers of *E. dulcis* (Burman f.) Trin. ex Henschel, $n =$ ca. 100, provide the familiar water chestnut of Oriental cuisine. The juice of the tubers is strongly antibiotic (Hegnauer). The species is closely related to the eastern North American *E. equisetoides*, and the pair serve as an example of the eastern Asian–eastern North American pattern of disjunction (Wood).

Species of ser. PAUCIFLORAE Svenson are tiny plants with few-flowered spikelets. *Eleocharis parvula* (Roemer & Schultes) Link, $2n = 8, 10$, *E. rostellata* Torrey, and *E. melanocarpa* Torrey occur in the Southeast, and all have broad ranges in our area.

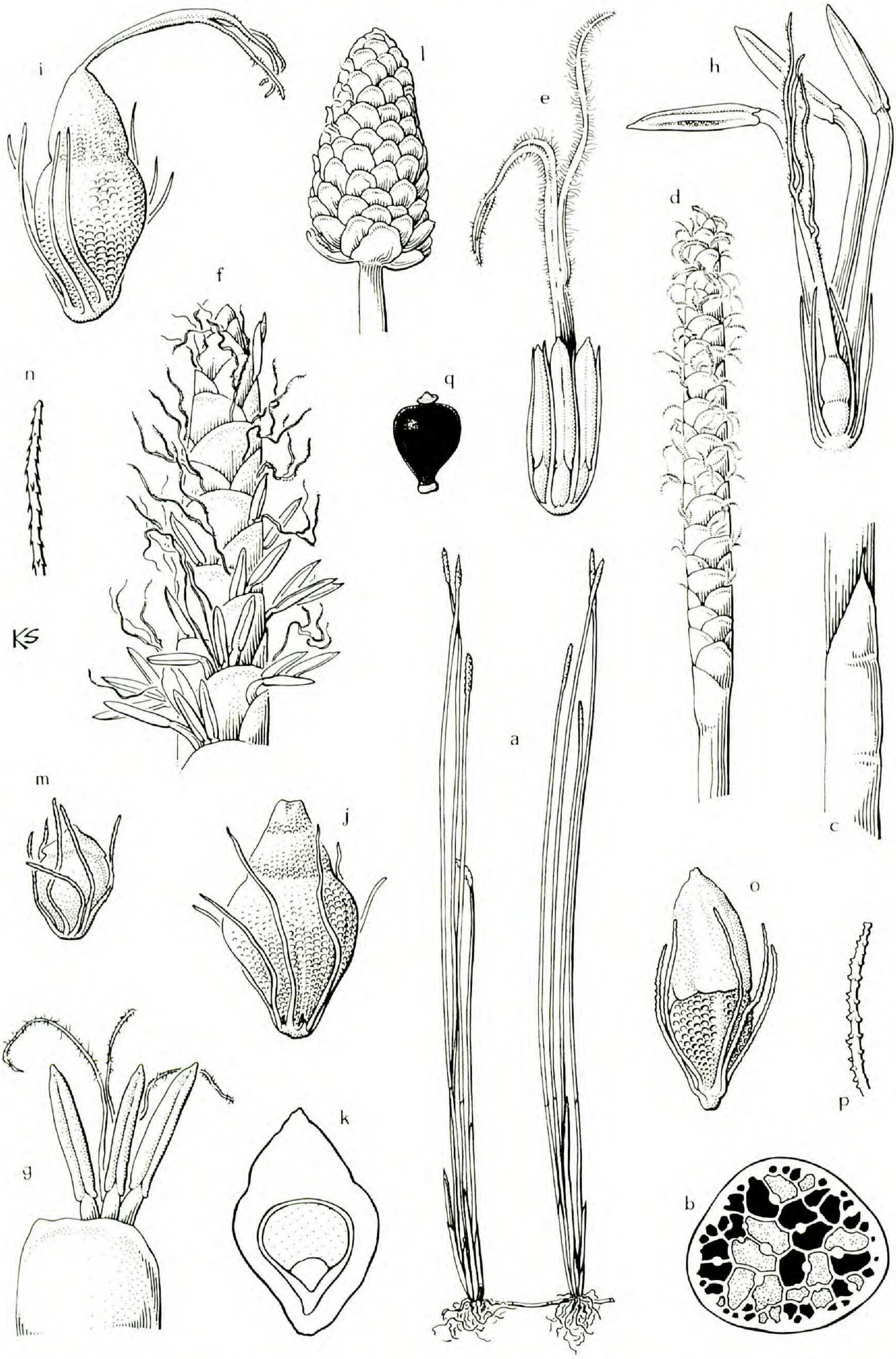

FIGURE 2. *Eleocharis*. a–k, *E. cellulosa:* a, habit of stoloniferous plants, × ¼; b, cross section of culm, showing air spaces (black) with cross partitions (stippled—cellular detail too small to be shown), × 10; c, detail of culm with apex of bladeless sheath, × 2; d, spike of flowers in carpellate phase (flowers protogynous), styles protruding (note flowers with either 2 or 3 stigmas), × 2; e, abaxial side of flower, stigmas receptive, filaments

Plants of ser. ACICULARES Svenson are also small. Three species occur in our area, and their contrasting distribution patterns are notable. The northern *Eleocharis Wolfii* Gray is found southward to Tennessee and Louisiana, while the neotropical *E. radicans* (Poiret) Kunth ranges northward to Virginia and Oklahoma. However, *E. acicularis* (L.) Roemer & Schultes, $2n = 20$, 30–38, 50–58, a widespread north-temperate species, is reported from throughout eastern North America. Both emergent and submersed growth forms of *E. acicularis* have been described. Submersed plants have three large lacunae per culm, while emergent plants have about ten small ones. These forms are genetically identical and fully interconvertible, as is demonstrated by reciprocal transplants (Rothrock & Wagner). The plants are able to grow in acidic runoff from Appalachian coal mines and flourish in streams with pH as low as 2.8. This is odd and suggests some overlooked variability in the species, because in northern Europe it nearly always occurs in basic waters (Iversen).

The plants of ser. OVATAE Svenson have broadly ellipsoid to ovoid spikelets. Three species are in our area: *Eleocharis obtusa* (Willd.) Schultes, $2n = 10$, in every Southeastern State, is one of the commonest spike-rushes in eastern North America; the closely related *E. Engelmannii* Steudel, $2n = 10$, occurs from Georgia and Missouri south to the Gulf Coast; and *E. lanceolata* Fern. is a southwestern species that just extends into our area in Arkansas and Louisiana.

Plants of ser. MACULOSAE Svenson are characterized by dark purple to black, biconvex achenes. Some species grow submersed, while others are found in littoral habitats. There are four species in our area: *Eleocharis caribbaea* (Rottb.) Blake is pantropic (northward to South Carolina and Texas); *E. olivacea* Torrey, $2n = 20$, is endemic to the Coastal Plain from Virginia to Florida; *E. atropurpurea* (Retz.) Kunth is widely but sporadically distributed in the Southeast (but otherwise is found throughout temperate and tropical regions of both the Old and New Worlds); and *E. flavescens* (Poiret) Urban is neotropical, growing north along the Coastal Plain to Delaware.

Plants of ser. WEBSTERIA (S. H. Wright) G. Tucker[6] are submersed, flaccid,

[6]*Eleocharis* ser. WEBSTERIA, comb. nov., based on *Websteria* S. H. Wright, Bull. Torrey Bot. Club **14:** 135. 1887.

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of stamens not yet elongated, 4 of 6 perianth bristles visible, × 10; f, apex of spikelet, carpellate phase past, lower flowers with protruding stamens, × 5; g, flower in staminate phase with apex of subtending scale, × 10; h, abaxial view of flower in staminate phase (note 4 of 6 perianth bristles, ovary with enlarged stylar base), × 10; i, adaxial view of mature achene with persistent stylar base and smooth perianth bristles, achene lenticular, × 12; j, mature achene, abaxial view, × 12; k, longitudinal cross section of achene (tubercle, pericarp, seed coat, and basal embryo unshaded, endosperm stippled), × 12. l–n, *E. obtusa:* l, spikelet with mature achenes (hidden by subtending scales, few stigmas visible at upper left), × 5; m, abaxial side of mature achene crowned by tubercle (persistent style base) and with perianth bristles, × 12; n, detail of perianth bristle to show retrorse barbs, × 25. o, p, *E. tuberculosa:* o, abaxial side of mature achene (trigonous in cross section) with tubercle, × 12; p, detail of perianth bristle, × 25. q, *E. atropurpurea:* abaxial side of mature achene (lenticular in cross section) with tubercle, perianth bristles absent, × 25.

slender-branched plants of shallow, still waters. There are one or perhaps two pantropic species (Eiten, 1976b). *Eleocharis confervoides*[7] is an uncommon plant of cypress swamps and lakes in Florida, southern Alabama, southern Georgia, and Louisiana. It is also known from widely scattered localities in the neotropics and in tropical Africa and Sri Lanka. The species has been variously placed in *Rhynchospora* Vahl (Bentham; Kükenthal, 1948), *Scirpus*, and the monotypic *Websteria*. The slender, leafless culms are similar to those of other species of *Eleocharis*. Additional submersed one-flowered species of *Eleocharis* occur in Brazil and Africa (Nelmes). At anthesis, the one-flowered spikelets of *E. confervoides* are exserted just above the water surface. The achenes lack the differentiated tubercle of most species of *Eleocharis*, but the embryos are typical of the genus (Van der Veken).

Rikli reported that the inner parenchymatous layer was absent from the bundle sheaths in many species of *Eleocharis*, a feature on which he based the segregate genus *Chlorocharis*. Metcalfe could not confirm this in any species including those investigated by Rikli but suggested that further study might be profitable.

Chromosomes of *Eleocharis* have been extensively studied. Cytologically, the genus is the best known in the Cyperaceae. Most species have the diffuse centric condition typical of the family; some have holocentric chromosomes (Battaglia). Although aneuploidy has been frequent in most other genera of Cyperaceae, polyploidy has been important in the evolution of this genus. Several species have tetraploid (and sometimes hexaploid) races or subspecies. Strandhede (1965, 1966) studied about 1100 European populations of species of ser. ELEOCHARIS (ser. *Palustriformes*) and reported that chromosome breakage and refusion were common. Most species had several cytotypes, and various kinds of multivalents were frequent at meiosis. Heterovalents formed in meiosis, and aberrant but apparently viable gametes were often observed. Similar reports of chromosomal variability have been made for North American species. Karyotypic rearrangements have been noted in *Eleocharis flavescens* (Poiret) Lam., which had 30 chromosomes in various combinations of univalents, bivalents, tetravalents, and ring complexes (Schuyler, 1977).

When the sample size is large, chromosome number can be correlated with morphology within species and between species pairs. For example, the European *Eleocharis uniglumis* (Link) Schultes consists of two subspecies that differ in ecology and in features of the spikelet scales. Subspecies *uniglumis* has $n = 46$, while subsp. *Sterneri* Strandhede has $n = 74–82$. Apparently, the latter taxon was derived from the former by tetraploidy followed by fusion of some of the chromosomes, but fusion of different chromosomes in different populations has also resulted in mixoploidy. In some cases affinities between species can be confirmed cytologically. For example, *E. Engelmannii* Steudel and *E. obtusa* are both $n = 5$ and have very similar karyotypes.

Species with different chromosome numbers are known to hybridize in the wild. Some hybrids (e.g., *Eleocharis mamillata* × *E. palustris* subsp. *palustris*)

[7] *Eleocharis confervoides* (Poiret) G. Tucker, comb. nov., based on *Scirpus confervoides* Poiret in Lam. Encycl. Méth. Bot. **6**: 755. 1804.

have greatly reduced fertility, while others (e.g., *E. palustris* subsp. *palustris* × subsp. *vulgaris*) have fertility comparable to that of the parent species.

Several species are important weeds, especially of rice fields.

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5. **Fimbristylis** Vahl, Enum. Pl. **2:** 285. 1805.

Small to medium-sized annuals or perennials of disturbed, open, wet habitats. Roots fibrous; rhizomes regularly present in some species. Culms slender, terete or nearly so, glabrous. Leaves all basal; sheaths smooth or pubescent, with ligule present or not, glabrous or ciliate; blades linear to filiform, flat, conduplicate, or involute, glabrous or pubescent, the margins glabrous or scabrellate; chlorenchyma radiate; bundle sheaths 3-layered ("*Fimbristylis* type"). Inflorescences terminal, branched (rarely sessile, capitate); bracts 1–6, erect to oblique, the sheaths greatly reduced to essentially absent, the blades leaflike; primary rays absent or 1–10, glabrous or scabrellate, secondary rays regularly produced in some species. Spikelets single or in clusters of 2–5, ovoid to lanceolate. Scales 5–100, ovate to oblong, obtuse or acute, blunt or mucronate [aristate], glabrous or puberulent abaxially, 1- to 5-nerved medially, nerveless laterally, deciduous at maturity. Flowers perfect. Perianth lacking. Stamens (1, 2, or) 3; filaments about as long as the subtending scales, flattened; anthers oblong, the apices of the connectives sometimes prolonged; pollen grains uniaperturate, obovoid,

subspheroidal, or spheroidal, scabrate, trinucleate. Styles slender, terete throughout or trigonous basally, usually fimbriate distally, deciduous from the mature achene; stigmas 2 (or 3), about as long as the style, glabrous. Achenes lenticular or trigonous, ovoid, oblong, or obovoid, the apex broadly rounded to subacute, apiculate or not, the base cuneate or stipitate, the surface smooth, warty, or reticulate with isodiametric or horizontally arranged rectangular cells, these cells concave or with a central papilla. Embryos turbinate, radicle lateral, coleoptile basal. Base chromosome number 5. TYPE SPECIES: *F. dichotoma* (L.) Vahl, *typ. cons.* (Name from Latin *fimbria,* fringe, and *stylus,* style, referring to the fringed style of most species.)

A genus of about 200 species, mainly pantropic but also well represented in warm-temperate regions. Most of the species grow in disturbed wet habitats, especially roadsides and croplands. The center of diversity is southeastern Asia (Goetghebeur & Coudijzer). Thirteen species are recorded from the United States. Twelve of these occur in the Southeast, while *Fimbristylis thermalis* S. Watson is endemic to California, Arizona, and Nevada (Kral). Kral's thorough monograph includes illustrations and chromosome counts for all species in North America.

Fimbristylis is closely related to *Bulbostylis* and *Abildgaardia.* Chromosome numbers in the three genera are based on five (Gordon-Gray, Kral), and their kranz anatomy is similar (three-layered bundle sheaths). Such anatomy is not reported in any other genera of the Cyperaceae (Metcalfe; Raynal, 1972). The three genera have been distinguished from the remainder of the Scirpeae as tribe Abildgaardiae Lye (Fimbristylideae Raynal).

Koyama (1961) treated *Bulbostylis* as a subgenus of *Fimbristylis,* while Kral recognized three genera, *Bulbostylis, Abildgaardia,* and *Fimbristylis.* Additional information supports Kral's belief. Gordon-Gray made a careful study of the southern African representatives of the three genera. *Abildgaardia* can be distinguished from *Bulbostylis* and *Fimbristylis* by its distichous spikelet scales. *Bulbostylis* and *Fimbristylis* are separated by a suite of characters. The embryos are consistently different (in *Fimbristylis* the radicle is lateral, the coleoptile basal; in *Bulbostylis,* the radicle is basal and the coleoptile lateral), although there is no single morphological character that separates the two genera. The styles of *Fimbristylis* are usually fimbriate (occasionally entire) and are deciduous, while those of *Bulbostylis* are always entire and have a persistent base. The spikelet scales of *Fimbristylis* are generally glabrous, while those of *Bulbostylis* are generally puberulent. The ligules of *Fimbristylis* are glabrous, while those of *Bulbostylis* are hispid. Species of *Fimbristylis* always lack intraprophyllar buds at the base of the inflorescence rays, while such buds are frequently present in *Bulbostylis* (Guaglianone). Species of the two genera differ in surface ornamentation of the achenes. Goetghebeur & Coudijzer examined about 100 species from throughout the world and found that the epidermal cells of *Fimbristylis* are horizontally elongate (infrequently isodiametric) and in vertical bands, but those of *Bulbostylis* are vertically elongate in horizontal bands. The two genera also differ in habit and habitat: *Fimbristylis* species are mostly perennials of moist soils, while *Bulbostylis* species are generally annuals of dry sandy soils.

Svenson recognized two sections in *Fimbristylis*; Kral did not comment on the infrageneric classification. Plants of sect. FIMBRISTYLIS (sect. *Dichelostylis* Bentham) have two stigmas, lenticular achenes, and styles commonly fringed apically. This section includes eleven of the fourteen species of the southeastern United States. Most of our species are somewhat weedy plants of disturbed wet habitats: *Fimbristylis tomentosa* Vahl, $n = 5$; *F. dichotoma* (L.) Vahl, $n = 10$, 15; *F. decipiens* Kral, $n = 10$; *F. annua* (All.) Roemer & Schultes, $n = 15$; *F. Vahlii* (Lam.) Link, $n = 10$; *F. puberula* (Michx.) Vahl, $n = 10$, 20; and *F. perpusilla* Harper, $n = 5$. In general these are widely distributed in the Southeast. *Fimbristylis perpusilla*, endemic to southeastern North America, is a notable exception. Kral knew of only two localities in southwestern Georgia for this tiny annual. Recently, the species has been reported in Horry County, South Carolina (Leonard) and in eastern Maryland (Schuyler, pers. comm.). The four remaining southeastern species of sect. FIMBRISTYLIS, *F. caroliniana* (Lam.) Fern. ($n = 10$, 20, 30), *F. schoenoides* (Retz.) Vahl ($n = 5$), *F. spathacea* Roth ($n = 24$), and *F. castanea* (Michx.) Vahl ($n = 10$), are tall plants of tidal marshes.

Plants of sect. TRICHELOSTYLIS Bentham have three stigmas, lenticular achenes, and entire styles. In our area this section is represented by *Fimbristylis autumnalis* (L.) Roemer & Schultes, *F. complanata* (Retz.) Link, and *F. miliacea* (L.) Vahl, all $n = 5$.

Fimbristylis autumnalis and *F. miliacea* are detrimental weeds in rice fields in the Southeast and California (Smith *et al.*), as well as in Asia and Africa (Holm *et al.*). *Fimbristylis tomentosa* is rapidly becoming a common weed in rice fields from South Carolina to Texas (Kral).

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6. **Bulbostylis** Kunth ex C. B. Clarke in Hooker f. Fl. Brit. India **6:** 651. 1983, *nom. cons.*

Small to medium-sized, tufted (solitary-stemmed) perennials or annuals of open or disturbed, dry or wet habitats. Roots fibrous; rhizomes lacking [present]. Culms slender, terete, glabrous. Leaves all basal; sheaths expanded basally or not, with ligule fimbriate or ciliate apically; blades filiform or narrowly linear, shorter than to slightly exceeding the culm, conduplicate or involute, often pubescent on one or both surfaces, the margins and midvein scabrellate or smooth; chlorenchyma radiate; bundle sheaths 3-layered ("*Fimbristylis* type"). Inflorescences terminal, capitate or branched; bracts 1–4, erect to oblique, shorter than to exceeding the length of the rays; primary rays lacking or 1–6, erect or spreading, subterete, glabrous or scabrellate, secondary rays absent. Spikelets solitary or in small clusters, ovoid to oblong or lanceolate. Scales 2–50, ovate to oblong, mucronulate, mucronate, or aristate, glabrous or scabrellate, or puberulent abaxially, 3- to 7-nerved, deciduous at maturity, the 1–4 lowest ones sterile. Flowers perfect. Perianth lacking. Stamens (1, 2, or) 3; filaments slender, hyaline, about as long as the subtending scales; anthers oblong, the apices of the connectives prolonged as tiny subulate tips; pollen grains uniaperturate, subspheroidal or obovoid, psilate or scabrate, trinucleate. Styles papillate, the bulbous basal portion persistent on the mature achene; stigmas 3, slender, glabrous, equaling to exceeding the style in length. Achenes trigonous (rarely biconvex), ovoid to oblong or ellipsoid, the apex obtuse to acute, crowned by the persistent bulbous style base, the base cuneate to stipitate, the surface smooth or reticulate with vertically elongate, rectangular (rarely isodiametric) cells, these cells smooth or sometimes with a single central papilla. Embryos turbinate, radicle basal, coleoptile lateral. Base chromosome number 5. TYPE SPECIES: *B. capillaris* (L.) C. B. Clarke, *typ. cons.* (Name from Latin *bulbus,* bulbous, and *stylus,* style, referring to the characteristic bulbous style base.)

A genus of about 120 species, mostly pantropic but with some in the warm-temperate regions. The genus is related to *Abildgaardia* and *Fimbristylis.* (A discussion of the distinguishing features of these genera appears under *Fimbristylis.*) *Bulbostylis* was first distinguished from *Fimbristylis* as the genus *Stenophyllus* Raf. (Neogenyton, 4. 1828). Although the generic name *Bulbostylis* Kunth was published in synonymy (Kunth) and validated by Clarke (q.v.), it has been conserved over *Stenophyllus.* Kral's illustrated monograph (including chromosome numbers) is the basic reference for the North American species.

Bulbostylis is represented in the United States by eight species, five of which occur in the Southeast. *Bulbostylis barbata* (Rottb.) C. B. Clarke, $n = 5$, *B. capillaris* (L.) C. B. Clarke, $n = 36$, and *B. ciliatifolia* (Ell.) Fern., $n = 30$, have each been reported from all or nearly all the southeastern states. *Bulbostylis stenophylla* (Ell.) C. B. Clarke and *B. Warei* (Torrey) C. B. Clarke, both $n =$

15, are more restricted in range than the three preceding species. Both occur along the Coastal Plain from Florida to North Carolina. Three more species, *B. Funckii* (Steudel) C. B. Clarke, $n = 10$, *B. juncoides* (Vahl) Kükenthal, $n = 60$, and *B. Schaffneri* (Boeck.) C. B. Clarke, occur in the Southwest. About 15 species occur in Mexico, Central America, and the West Indies, with perhaps 20 in all of South America. The center of diversity for the genus is tropical Africa, where 30–40 species are reported.

The southeastern species of *Bulbostylis* are generally found in open, dry, sandy places, such as pine flatwoods, sand hills, palmetto scrub, roadsides, and shores. They are annuals or short-lived perennials. The neotropical *B. paradoxa* (Sprengel) Lindm., a long-lived perennial that flowers in response to fires (Kral), occurs in pinelands and savannas in Cuba and from Mexico to northern South America.

Plants with basal clusters of spikelets are occasionally encountered in several species of *Bulbostylis* (e.g., *B. capillaris* and *B. Funckii*). Formation of such spikelets may be the result of drought, but no studies have been made to document this supposition. In some species achenes produced by the basal spikelets are 1½–2 times larger than those produced by typical elongate culms. Such amphicarpy has also been reported in certain African species (Haines).

Bulbostylis barbata is a weed of old fields and sandy croplands in the southeastern Coastal Plain. Three species (including *B. barbata*) are reported as significant weeds in tropical Africa and Asia (Holm *et al.*).

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7. **Abildgaardia** Vahl, Enum. Pl. **2:** 296. 1805.

Small, single-stemmed or tufted, bulbous-based, glabrous perennials of tropical and subtropical grasslands. Roots fibrous; rhizomes lacking. Culms subterete, smooth. Leaves about ½ as long as the culms; sheaths expanded, their overlapping bases forming the bulblike base of the plant, ligules lacking; blades linear-filiform, slightly involute, thickened at margins, scabrellate distally; chlorenchyma radiate; bundle sheaths 3-layered ("*Fimbristylis* type"). Inflorescences simple cymes of 1–3[–6] sessile or pedunculate spikelets; bracts sol-

itary, filiform. Spikelets broadly lanceolate, slightly compressed, the scales distichous or essentially so. Scales 3–15, ovate, acute, mucronate, 3- to 5-nerved medially, nerveless laterally, deciduous as the achenes mature. Flowers perfect (although frequently the distal flowers of a spikelet staminate only). Perianth lacking. Stamens (1, 2, or) 3; filaments flattened; anthers linear, the apices of the connectives not prolonged; pollen grains uniaperturate, obovoid to subspheroidal, scabrate, trinucleate. Style trigonous basally, slender and capillary distally, deciduous from the mature achene; stigmas 3, linear, about as long as the style, glabrous. Achenes rounded-trigonous, ovoid, the apex broadly rounded, apiculate, the base abruptly contracted to a stipe, the surface pebbled. Embryo turbinate, radicle basal. Base chromosome number 10. (Named for P. S. Abildgaard, an eighteenth-century Danish botanist.) TYPE SPECIES: *A. ovata* (Burman f.) Kral (*Carex ovata* Burman f.; *A. monostachya* (L.) Vahl); see Britton & Millspaugh, Bahama Fl. 52. 1920.

A pantropic genus of about 15 species, distinguished from *Bulbostylis* and *Fimbristylis,* with which it has been united, by its distichous spikelet scales and its deciduous style bases. Chemical data support the recognition of *Abildgaardia.* The four Australian species produce the flavones luteolin and tricin, whereas the 15 species of *Fimbristylis* and *Bulbostylis* examined had only tricin (Harborne *et al.*).

Abildgaardia is represented in the New World by two species. *Abildgaardia mexicana* (Palla) Kral, $n = 10$, is endemic to grasslands of the Mexican High Plateau. The southeastern representative, *A. ovata, n* = 10, occurs in Florida, the West Indies, and the lowlands of Central and South America. *Abildgaardia ovata* is found in grasslands over limestone in southern Florida (Dade and Monroe counties) and in the vicinity of Tampa (Citrus County; Kral).

Species of *Abildgaardia* have no reported economic significance. None has been noted as a weed.

REFERENCES:

Under family references see BARROS (1945); BENTHAM; CLARKE (1908); GODFREY & WOOTEN; HARBORNE; HARBORNE *et al.*; HUANG; KUNTH; LERMAN & RAYNAL; METCALFE; NAPPER (1965); NEES VON ESENBECK; O'NEILL; SCHULZE-MOTEL (1959, 1964); and VAN DER VEKEN.

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Tribe CYPEREAE

8. **Cyperus** Linnaeus, Sp. Pl. **1:** 44. 1753; Gen. Pl. ed. 5. 27. 1754.

Tufted or rhizomatous, perennial or less often annual herbs of disturbed wet to dry soils, marshes, ditches, shallow swamps, and shores in full sun or light shade. Roots fibrous; rhizomes or stolons sometimes present, horizontal to oblique. Culms trigonous (sometimes with winged angles) or terete, smooth or scabrellate. Leaves all basal; sheaths glabrous, sometimes with conspicuous

cross veins, especially in emergent plants, ligule present or lacking; blades linear to lanceolate, flat, conduplicate, plicate, filiform, crescentiform, or involute, the margins and midvein usually scabrellate; stomata paracytic, sometimes surrounded by 1–4 papillae; chlorenchyma radiate or not (if radiate the bundle sheaths 2-layered—"*Cyperus* type"). Inflorescences terminal, diffusely branched, spicate, or capitate; bracts (1–)3–6(–22), the sheaths very short, the blades leaflike, closely spaced and appearing verticillate at the apex of the culm, usually ascendent but in some species erect (the inflorescence thus appearing lateral), horizontal, or reflexed, forming a conspicuous involucre; rays glabrous (rarely scabrellate or hispidulous), unequal in length, produced singly from the axils of the inflorescence bracts; spikes digitate, glomerulate, or spicate; rachis smooth, rarely scabrellate. Spikelets (1–)5–30(–150), cylindrical to compressed, ovate, lanceolate, or linear, the scales distichous; rachilla deciduous or persistent, internodes winged or wingless, spongy and thickened in a few species. Scales (1 or) 2–20(–80), oblong, elliptic, or ovate, obtuse, acute, mucronulate, or cuspidate, 3- to 11-nerved, deciduous or persistent, the 2 lowermost (bract and prophyll) sterile. Flowers perfect [imperfect, the plants dioecious]. Perianth lacking. Stamens (1, 2, or) 3; filaments ribbonlike, usually as long as the subtending scales; anthers ovoid, ellipsoid, or linear, the apices of the connectives sometimes prolonged as small, reddish, entire or scabrellate appendages; pollen grains obovoid, subspheroidal, rectangular, or triangular, (1- or) 4-aperturate, psilate, trinucleate. Styles slender, the base sometimes persistent as an apiculus or beak on the mature achene; stigmas capillary, shorter than, equaling, or exceeding the style in length, glabrous [glandular]. Achenes trigonous or lenticular, ovoid, ellipsoid, or narrowly oblong, obtuse or acute, apiculate or not, stipitate, substipitate, or sessile, smooth, puncticulate, or reticulate. Embryos broadly to narrowly ellipsoid. Base chromosome number 8. (Incl. *Pycreus* Beauv., *Mariscus* Vahl, *Juncellus* (Griseb.) C. B. Clarke, *Acorellus* Palla, *Remirea* Aublet, *Torulinium* C. B. Clarke.) LECTOTYPE SPECIES: *C. esculentus* L.; see Britton & Brown, Illus. Fl. No. U.S. Canada, ed. 2. **1**: 297. 1913. (Name from Greek *kupeiros*, ancient name for *C. longus* L.)—FLAT-SEDGE, UMBRELLA-SEDGE, SEDGE-GRASS, GALINGALE (Britain).

A very large genus of about 650 species widely distributed throughout the tropical and warm- and cool-temperate regions of the world. It is the second largest genus of the Cyperaceae; only *Carex* L. is larger. *Cyperus* is morphologically coherent and is readily recognized by the distichous arrangement of scales on the spikelets. Six subgenera have been recognized: subg. CYPERUS, subg. PYCNOSTACHYS C. B. Clarke,[8] subg. PYCREUS (Beauv.) Gray,[9] subg. JUNCELLUS (Griseb.) Kükenthal, subg. TORULINIUM (Desv.) Kükenthal, and subg. FIMBRICYPERUS K. A. Lye. These are circumscribed by features of the achenes, spikelets, and vegetative anatomy. Most recent workers have followed

[8]*Cyperus* subg. PYCNOSTACHYS C. B. Clarke in Hooker f. Fl. Brit. India **6**: 597. 1893. LECTOTYPE SPECIES (here designated): *C. diffusus* Vahl. Synonym: *Cyperus* subg. *Protocyperus* K. A. Lye, Nordic Jour. Bot. **1**: 54. 1981. TYPE SPECIES: *C. difformis* L.

[9]*Cyperus* subg. PYCREUS (Beauv.) Gray, Man. Bot. ed. 1. 517. 1848. This combination is consistently, but erroneously, attributed to C. B. Clarke, Jour. Linn. Soc. Bot. **21**: 33. 1884.

Kükenthal and Fernald, who treated the genus in the broad sense. Others (Koyama, 1962b; Vorster; Raynal, 1972, 1973) have followed Clarke (1908) and recognized the subgenera as genera. Subgenera PYCREUS and JUNCELLUS differ from the others in having the derived conditions of lenticular (vs. trigonous) achenes and bifid (vs. trifid) styles (Blaser, 1941a; Raynal, 1972). In subg. PYCREUS the achenes are laterally compressed, while in subg. JUNCELLUS the compression is dorsiventral, suggesting that the bicarpellate condition evolved twice. Several other genera of the family (e.g., *Carex* and *Bulbostylis*) are divided into subgenera on the basis of carpel number.

Subgenus TORULINIUM differs from all other subgenera in having the rachilla articulate at the base of each scale (i.e., an abscission layer forms) (vs. continuous or articulate only at the base of the spikelet). Thus, the mature spikelet of plants of subg. TORULINIUM breaks up into one-fruited segments, each consisting of an internode of the rachilla, a scale, and an achene.

Subgenera JUNCELLUS, PYCREUS, and TORULINIUM are readily distinguished from each other and from the remaining subgenera. However, the subgeneric classification of the remaining species of the genus has been a matter of long debate. Traditionally, the species here recognized as constituting subgenera PYCNOSTACHYS and CYPERUS (Lye, 1981) have been circumscribed differently as subgenera *Mariscus* and CYPERUS. Clarke (1908) and Kükenthal (1935–1936) defined subg. CYPERUS as differing from subg. *Mariscus* in having the spikelet rachilla firmly attached to the rachis, while the scales are deciduous, falling from the rachilla as the achenes mature. In species of subg. *Mariscus,* the scales remain firmly attached to the rachilla even after the spikelet has fallen from the rachis. O'Neill (1942) listed some twenty species (e.g., *Cyperus strigosus* L., a common species throughout the United States) having characteristics of both subgenera—both the rachillas and the scales are more or less deciduous. Kükenthal placed such intermediate species in his concept of subg. *Mariscus,* but they are clearly transitional between subg. CYPERUS and subg. *Mariscus.* Also, as O'Neill (1942) observed, *C. rotundus* L. and *C. esculentus* L., both of which have always been placed in subg. CYPERUS, have persistent scales, a feature attributed solely to subg. *Mariscus* by Kükenthal. Federowicz surveyed the epidermal features of leaves and achenes of both subgenera and found no consistent differences between the two. There is no single character that consistently separates them. O'Neill (1942, p. 47) stated: "It is ill-advised to maintain *Mariscus* as a genus when it is very ill-defined even as a subgenus." More recently, Koyama (1962b) and Vorster have recognized *Mariscus* at the generic level.

Rikli surveyed the anatomy of the leaves and culms of many genera of the Cyperaceae. He divided *Cyperus* into two genera, *Eucyperus* (= *Cyperus*) and *Chlorocyperus.* The latter was characterized by having radiate chlorenchyma (i.e., kranz anatomy), while the former had nonradiate. Lerman & Raynal examined the distribution of the C_4 photosynthetic pathway in the family and found that *Cyperus* contained both C_3 and C_4 species. These physiological differences were correllated with the division that Rikli had based on anatomical information. Subgenus PYCNOSTACHYS corresponds to "Pars Pycnostachys" (not a valid taxonomic rank) in Kükenthal's monograph of the genus. Lye

concurred with O'Neill that *Mariscus* could not be maintained even at the subgeneric rank but ought to be included in subg. CYPERUS. The recognition of subgenera PYCNOSTACHYS and CYPERUS (rather than subgenera *Mariscus* and CYPERUS *sensu* Kükenthal) is a natural classification that reflects current knowledge of the phylogeny of the genus, as outlined by Raynal (1973).

Van der Veken surveyed variation in embryo shape within the subfamily, including 162 species of *Cyperus*. Throughout this genus the embryos were broadly ellipsoid. There were interspecific differences in size, but these did not follow taxonomic lines. Van der Veken's data supported a broad concept of the genus.

Harborne and colleagues surveyed the distribution of flavonoids in South American, African, and Australian species of *Cyperus*. They examined about 150 species and reported that each subgenus had a distinct profile of compounds. Subgenus PYCNOSTACHYS is characterized by flavonols, which are absent in the other subgenera (these have flavones instead). Aurones, which give a yellowish hue to the inflorescences, are present in subgenera CYPERUS (including subg. *Mariscus*) and TORULINIUM but lacking in subgenera PYCREUS and PYCNOSTACHYS. These investigators believed the differences they reported confirmed the recognition of PYCNOSTACHYS as a subgenus distinct from subg. CYPERUS. They also concluded that the flavonoid data indicated that no subgenus was sufficiently unlike the others to merit generic status. Thus, these authors also favored a broad concept of the genus.

Chromosome numbers have been reported for about 40 species of *Cyperus*. However, even this limited number of counts gives some information about evolution in the genus. One significant trend is that subg. PYCNOSTACHYS has haploid numbers from 8 to 28 (mostly 15–20), while subg. CYPERUS has n = 8–86 (mostly 45–60). The generally lower chromosome numbers of subg. PYCNOSTACHYS suggest that it is the most primitive subgenus; this is also indicated by its being the only subgenus with the C_3 pathway. Different chromosome numbers have been reported for several species. In some species (e.g., *C. rotundus*, n = 16, 48, 54, 76) polyploid races are indicated; in others (e.g., *C. Houghtonii* Torrey, n = 84, 85, 86), mixoploid.

Cyperus in the southeastern United States comprises 63 species in four subgenera: five species are adventives from the Old World, seven are endemic, 17 are shared with the northeastern states, 15 are shared with the neotropics, and the remaining ones have either pantropic or cosmopolitan distributions.

Subgenus PYCNOSTACHYS (C_3 photosynthesis, spikelets in glomerules or digitate clusters, achenes trigonous), with 150 species worldwide (Lye), includes 14 in our area. Eight of these belong to the New World sect. LUZEOLOIDEI (Kunth) Clarke (spikelets in glomerulate clusters, scales with proximal abaxial groove, stamen one per flower). The group has been revised by Denton (1978, 1983), who has also investigated the morphology of the achenes and leaf blades. She showed that epidermal features of the achenes could be used to distinguish species. Only one chromosome count is available for this section: *Cyperus Eragrostis* Lam., $2n$ = 42. This species has been collected as a waif in South Carolina; it is native to the Pacific coast of the United States and temperate South America and is naturalized in southern Europe and southeastern Texas.

The remaining six southeastern species of the subgenus are scattered among four sections. Section HASPANI (Kunth) Clarke[10] (wetland plants; spikelets digitate; achenes ovoid, papillose), is represented in our area by three species. *Cyperus Haspan* L. occurs in Coastal Plain wetlands from Virginia southward. It is one of the few truly pantropic species and is believed to be native to southeastern Asia, tropical Africa, and the New World tropics. *Cyperus dentatus* Torrey, $2n = 34$, is a northeastern species of pond shores that extends southward to South Carolina and Tennessee. This is the only species of the subgenus with tuberiferous stolons. It is closely related to the southeastern endemic *C. Lecontei* Torrey ex Steudel,[11] a Coastal Plain species ranging from North Carolina to Louisiana.

Section FUSCI (Kunth) Clarke[12] (plants annual; scales ovate; styles and stigmas very short; achenes ovoid, glossy) is represented in the Southeast by one introduced species. *Cyperus difformis* L., $2n = 34$, a weedy Asian species, was first collected in the eastern United States in Norfolk Co., Virginia, in 1935 by Fernald (Tyndale). Lipscomb (1980b) has provided an interesting account of the spread of this species in North America. The species was first collected in the New World in New Mexico in 1850. It is a significant weed of rice fields in California but has not yet become a problem in the southern rice-producing states (Bryson). In contrast to the other weedy species of the genus (e.g., *C. esculentus*), *C. difformis* is an annual that is capable of completing its life cycle in only one month; a single plant can produce thousands of achenes. The species is adapted to ground that is frequently flooded, such as rice fields. The seeds germinate best under shallow water (McIntire). The type species of the section, *C. fuscus* L., $2n = 72$, is Eurasian; it is sparingly adventive from Massachusetts to Nebraska and Virginia but has not yet been reported from the Southeast.

Subgenus PYCREUS is characterized by having lenticular, laterally compressed achenes and C_4 photosynthesis. There are about 120 species worldwide, of which eight occur in our area. All our species are fibrous-rooted annuals, mostly less than 30 cm tall, of disturbed wet soils. One, *Cyperus louisianensis* Thieret, is endemic to southeastern Louisiana. Five pantropic species occur in our area: *C. flavescens* L., $2n = 50$, *C. pumilus* L., $2n = 94$, *C. flavicomus* Michx. (*C. albomarginatus* "Nees," see Tucker, 1985a), *C. polystachyos* Rottb., and *C. lanceolatus* Poiret. *Cyperus bipartitus* Torrey (*C. rivularis* Kunth, see Tucker, 1983a), $n = 27$, is a widespread North American species that also occurs in the mountains of Mexico, Central America, and southern South America (Tucker, 1983a). *Cyperus filicinus* Vahl is endemic to eastern North America (tidal marshes from Maine to Louisiana).

Subgenus JUNCELLUS has only about six species worldwide. The pantropic *Cyperus laevigatus* L., $2n = 80$–84, was collected as a ballast plant in Wilmington, North Carolina (*G. McCarthy s.n.* in 1888, GH!). It apparently never

[10]*Cyperus* sect. HASPANI (Kunth) Clarke, Jour. Linn. Soc. Bot. **21**: 119. 1884. TYPE SPECIES: *C. Haspan* L.

[11]The name has been attributed to Torrey, but he published it provisionally under *C. dentatus* var. *multiradiatus* Torrey (Ann. Lyc. Nat. Hist. New York **3**: 273. 1836). The name *C. Lecontei* was first validly published by Steudel (Syn. Pl. Glum. 2: 17. 1854).

[12]*Cyperus* sect. FUSCI (Kunth) Clarke, Jour. Linn. Soc. Bot. **21**: 131. 1884. TYPE SPECIES: *C. fuscus* L.

became established in the eastern United States. This species, which grows in alkaline or brackish soils, is native to the area from western Texas to southern California and southern Mexico, to the Lesser Antilles, and to South America.

Subgenus CYPERUS contains about 400 species worldwide and about 35 in the Southeast. Among these are pantropic, neotropical, and cosmopolitan representatives. About half of the 35 are endemic to the United States, and many of these are endemic to the Southeast; four are introduced from the Old World.

Plants of sect. UMBELLATI C. B. Clarke are characterized by their caespitose habit, deciduous rachillas, and appressed, mostly persistent scales. This pantropic group has twelve species in the southeastern United States: *Cyperus croceus* Vahl (*C. globulosus* auct., non Aublet), *C. echinatus* (L.) Wood (*C. ovularis* (Michx.) Torrey), *C. Plukenetii* Fern., *C. ovatus* Baldwin (*C. Pollardii* Britton), *C. hystricinus* Fern., *C. refractus* Torrey, *C. retrofractus* (L.) Torrey (*C. dipsaciformis* Fern., see Carter & Jarvis), *C. lancastriensis* Porter, *C. retrorsus* Chapman (*C. Nashii* Britton), n = ca. 90 (Marcks, 1972a), *C. thyrsiflorus* Jungh., *C. retroflexus* Buckley (*C. uniflorus* Torrey & Hooker, non Thunb.), and *C. lentiginosus* Millsp. & Chase. Carter (1984) revised the North American representatives, some of which were also studied by Marcks (1972b) and Tucker (1983a, 1985b).

Plants of sect. LAXIGLUMI[13] are characterized by their rhizomatous, single-stemmed habit, deciduous rachillas, and spreading, more or less deciduous scales. Species of this section infrequently hybridize with those of the preceding one (Marcks, 1972a, 1972b). Eight species occur in the eastern United States, of which four are in our area; there are ten in the mountains of the southwestern United States, Mexico, and Central and South America. The plants typically grow in open, dry, sandy or gravelly habitats. The American species were studied biosystematically by Marcks (1972a, 1972b), and the Mexican and Central American ones by Tucker (1983a, 1984, 1985a). The species are cytologically similar: all are n = 82 except *Cyperus Schweinitzii* Torrey, n = 84, 85 (Marcks, 1972b). *Cyperus filiculmis* Vahl (*C. Martindalei* Britton), *C. lupulinus* (Sprengel) Marcks (*C. filiculmis* auct., non Vahl), *C. Grayi* Torrey, and *C. Grayoides* Mohlenbrock occur in our area.

The remaining southeastern species are scattered among six mainly pantropic sections. Section CYPERUS (sects. *Esculenti* Kükenthal and *Rotundi* C. B. Clarke) is most diverse in Australasia (Blake, J. H. Kern). In members of this section both the scales and the spikelets are persistent (a combination of characters unknown elsewhere in the genus), and the stolons are tuberiferous. *Cyperus rotundus* L., purple nut-sedge, is generally acknowledged to be the world's worst weed. It occurs throughout the Southeast, except in the mountains, but extends only as far north as southern Missouri and southeastern Virginia. It does not grow north of the mean 1°C January isotherm (Stoller). *Cyperus esculentus* L., yellow nut-sedge, is able to tolerate winter air temperatures as low as −18°C and is a serious weed in much of the world, especially in cooler regions where

[13] *Cyperus* sect. LAXIGLUMI (C. B. Clarke) Kükenthal, Pflanzenr. IV. **20**(Heft 101): 220. 1936; based on *Mariscus* subsect. *Laxiglumi* C. B. Clarke, Kew Bull. Add. Ser. **8:** 103. 1908, "*Laxiglumae.*" LECTOTYPE SPECIES (here designated): *Mariscus Manimae* (HBK.) C. B. Clarke (= *C. Manimae* HBK.).

the more tropical *C. rotundus* does not grow. These two species also differ in their thermal optima for growth. In Mexico *C. esculentus* is found from sea level to about 2600 m, while *C. rotundus* occurs from sea level to about 1500 m (Tucker, 1985b). It is unclear whether these species are native to the New World. *Cyperus esculentus* now occurs in all 50 states and in southern Canada.

The stoloniferous nature of these two species underlies their success as weeds. A single tuber can produce a population covering 2–4 m^2 in two months (Horowitz). The sharp-pointed stolons can cause puncture wounds in the hands of farm workers and curious agronomists and penetrate root crops such as potatoes and yams. In 1821 Elliott noted that *Cyperus rotundus* was a great problem for farmers in Georgia and South Carolina. He outlined a method for removing an infestation by cultivating a fallow field weekly for a year (including winter), thus allowing the tubers to be killed by exposure to drying and cold air. Mulligan & Junkins provided a thorough summary of its biology, emphasizing weed control and management. Horak & Holt analyzed isozymes in ten widely separated populations of *C. esculentus* in California. Genetic variation served to determine the relative importance of sexual and asexual reproduction. Results indicated that reproduction by seeds is unimportant in maintenance of populations in croplands. Stolons and tubers are the primary means of reproduction. Germinability of seeds from northeastern populations ranged from 7 to 95 percent; such variation was believed to be genetic (Mulligan & Junkins). Seeds from a 50-year-old herbarium specimen had 5 percent germination (Mulligan & Junkins). *Cyperus esculentus* is self-incompatible (Horak & Holt).

Members of sect. COMPRESSI Nees[14] are caespitose annuals with cuspidate scales and emarginate achenes. Most of the species are native to the Old World tropics. The pantropic *Cyperus compressus* L., $n = 64$, is the only representative in the United States. It is found throughout the Coastal Plain and Piedmont, as far north as Pennsylvania and Missouri. The only other New World species, *C. Wilburii* G. Tucker, is endemic to the lowlands of southern Mexico. Its larger size suggests that it may be a tetraploid derived from *C. compressus*.

Section IRIOIDEI Nees[15] comprises several tropical and temperate eastern Asian species. The plants are annual and have ascending-appressed spikelets and three-nerved, orbiculate scales. *Cyperus Iria* L. is an adventive in all tropical and temperate regions of the New World and is a common weed throughout the southeastern Coastal Plain and Piedmont. Apparently, the plants are cleistogamous. The staminal filaments elongate only enough to bring the minute anthers into contact with the very short stigmas, which remain inside the scales at anthesis. Often the anthers are later found agglutinated to the stigmas.

Section VISCOSI C. B. Clarke[16] is endemic to the New World and is represented

[14]*Cyperus* sect. COMPRESSI Nees, Linnaea **9:** 234. 1834. TYPE SPECIES: *C. compressus* L.

[15]*Cyperus* sect. IRIOIDEI Nees, Linnaea **9:** 235. 1834. TYPE SPECIES: *C. Iria* L. Synonym: sect. *Iriae* (Kunth) C. B. Clarke, Kew Bull. Add. Ser. **8:** 99. 1908.

[16]*Cyperus* sect. VISCOSI C. B. Clarke, Jour. Linn. Soc. Bot. **21:** 114. 1884. TYPE SPECIES: *C. viscosus* Aiton (= *C. elegans* L.). Synonym: sect. *Glutinosi* (Böck.) Kükenthal, Pflanzenr. IV. **20**(Heft 101): 163. 1936.

by two species in the Southeast. Plants of this section have spicate inflorescences; the spikes are short and dense and appear glomerulate, which apparently caused Kükenthal to believe them to be closely related to plants of sect. LUZEOLOIDEI (subg. PYCNOSTACHYS). The plants have kranz anatomy, further supporting their placement in subg. CYPERUS (Tucker, 1985b). They secrete a viscid fluid and are sticky when living, hence the appropriate sectional name. Two species occur in the Southeast. *Cyperus elegans* L. grows from southern Florida and Texas south to Ecuador. *Cyperus oxylepis* Nees ex Steudel is a South American species that has recently become an adventive in the United States, where it was first noted in Texas (O'Neill). More recently it has been reported in Louisiana (Thieret, 1964) and in Charleston County, South Carolina (*MacDougal 1501*, 5 Aug. 1981, DUKE, NCU, NYS).

Subgenus TORULINIUM has a single representative in our area, the pantropic and warm-temperate *Cyperus odoratus* L. It is a common species of disturbed, wet soils, especially pond shores and stream banks. Five segregate species (e.g., *C. Engelmannii* Steudel, *C. ferruginescens* Böck.) have been recognized at various subspecific ranks. Evidence for treating these segregates as conspecific with *C. odoratus* has been published (Tucker, 1984). Three other species of this subgenus occur in the New World tropics: *C. Correllii* (Koyama) G. Tucker in the Bahamas, *C. rhizophorae* (C. B. Clarke) Standley along the Pacific Coast of Central America, and *C. filiformis* Sw. in the Greater and Lesser Antilles.

Section REMIREA (Aublet) Kern contains a single pantropic species, *Cyperus pedunculatus* (R. Br.) Kern (*Remirea maritima* Aublet), beach-stars. In our area it occurs only in Peninsular Florida. The rhizomatous plants form mats that bind sand dunes. This species has been treated as constituting a monotypic genus, *Remirea*, which Kükenthal placed in the Rhynchosporoideae. Metcalfe and Oteng-Yeboah showed convincingly that the anatomy of *C. pedunculatus* is similar to that of the kranz species of *Cyperus*. Within *Cyperus*, the thickened upper internode ("corky organ") of the one-flowered spikelets suggests a relationship with subg. TORULINIUM (*C. odoratus* typically has spongy, thickened rachilla internodes). Such internodes may serve to make the achenes buoyant, thus contributing to dispersal by water, but experimental evidence for this supposition is lacking.

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9. **Kyllinga** Rottboell, Descr. Icon. Rar. Nov. Pl. 12. 1773, *nom. cons.*

Small, rhizomatous or tufted perennials (1 species annual). Culms trigonous or roundly trigonous, smooth. Leaves 1–5, basal; sheaths short, closely fitting the culms, ligule lacking; blades flat or V-shaped in cross section [lacking], the margins and keels scabrellate, especially distally; chlorenchyma radiate; bundle sheaths 2-layered ("*Cyperus* type"). Involucral bracts 2–4, leaflike, horizontal to slightly reflexed or erect. Spikes 1–4, sessile, densely ovoid to cylindrical. Spikelets 15–150 per spike, not readily distinguishable without magnification, ovate to lanceolate, decidedly flattened. Scales 4, the 2 basal minute, the 2 distal much longer, making up the bulk of the spikelet, the lower of these (the third scale of the spikelet) subtending a perfect flower, the upper (fourth scale) slightly smaller, sterile or infrequently bearing 1 or 2 (often abortive) stamens. The fertile scale of the spikelet ovate, conduplicate, with a conspicuous smooth or spinulose-scabrellate [fimbriate or erose] keel terminating in a mucronate or mucronulate [aristate] apex, laterally 2- to 4-nerved. Flowers perfect. Perianth lacking. Stamens 1–3; filaments ribbonlike, about as long as the subtending scales; anthers oblong-elliptic to linear, the apices of the connectives not prolonged; pollen grains 4-aperturate [uniaperturate], obovoid, psilate, trinucleate. Styles capillary, smooth; stigmas 2, about as long as the styles. Achenes lenticular, laterally compressed, narrowly ovoid to oblong or ellipsoid, about ½ the length of the subtending scale, the apex obtuse, apiculate, the base cuneate to rounded, barely to decidedly stipitate, the surface puncticulate. Embryos narrowly ellipsoid. Base chromosome number 60. (*Cyperus* subg. *Kyllinga* (Rottb.) Valck.-Suringar.) TYPE SPECIES: *K. monocephala* Rottb., *nom. illeg.* (= *K. nemoralis* (J. R. & G. Forster) Dandy ex Hutchinson & Dalz., *typ. cons.*). (Named for Peter Kylling, Danish botanist, d. 1696.)

A genus of about 40–45 species, nearly all of which are tropical. The greatest diversity is in tropical East Africa and Madagascar, where there are 30–35 species. Eight occur in southern Asia, three or four in eastern Asia, and two in Australasia. Two (neither endemic) grow in the Hawaiian Islands, but none occurs in Europe. There are eight species in the New World; three of these, *Kyllinga pumila* Michx., *K. odorata* Vahl, and *K. brevifolia,* $2n = 120$, which occur in the Southeast, are pantropic. *Kyllinga vaginata* Lam. and *K. tibialis* Ledeb. are species of littoral habitats in the Caribbean, South America, and tropical West Africa. *Kyllinga nudiceps* C. B. Clarke is endemic to Isla del Coco, in the Pacific some 300 km southwest of Costa Rica. *Kyllinga squamulata* Thonn. ex Vahl (*Cyperus Metzii* Mattf. & Kükenthal), from tropical Asia, is introduced in Florida and the West Indies; *K. brevifolioides* (Delahoussaye & Thieret) G. Tucker,[17] from temperate eastern Asia, has become sparingly established in the eastern United States in the area from Connecticut to western North Carolina and Tennessee. The four southeastern species are mostly weedy plants of disturbed, usually moist, sunny places. *Kyllinga pumila* is a common

[17] *Kyllinga brevifolioides* (Delahoussaye & Thieret) G. Tucker, comb. nov., based on *Cyperus brevifolioides* Delahoussaye & Thieret, Sida **3**: 131. 1967.

weed of lawns and croplands in the eastern United States from Pennsylvania and Missouri south to the Gulf Coast.

Kyllinga differs from *Cyperus,* with which it has been combined by some workers, in its very short rachilla and in the two lowest sterile scales of its spikelets being greatly reduced. Taxonomically useful characters have been reviewed by Tucker. The most important of these are habit (rhizomatous perennials or caespitose annuals), length and orientation of the involucral bracts, and length of the anthers. Such characters as number of stamens and presence of spinulose prickles on the keels of the scales have previously been used (Delahoussaye & Thieret) but frequently vary within individuals of the same species and sometimes within spikes of a single plant.

The plants are probably at least partly wind pollinated. However, because of the close spacing of the spikelets within an inflorescence, some anthers probably shed their pollen directly onto stigmas of adjacent spikelets. Insect pollination may be important in some species with conspicuous, whitish or cream-colored spikes (e.g., *Kyllinga odorata*), as it is in many species of *Rhynchospora* sect. DICHROMENA. Syrphid flies have been observed visiting individuals of *K. tibialis* in Costa Rica (*MacDougal 1190,* DUKE) and *K. odorata* in Mexico (*Tucker 2222,* DUKE).

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10. **Lipocarpha** R. Brown in Tuckey, Narr. Exped. Congo **5:** 459. 1818, *nom. cons.*

Small, caespitose annuals of wet sandy or peaty soils. Roots fibrous, rhizomes absent. Culms 1–20(–100), usually densely clustered, erect, spreading, or curved,

filiform, terete, glabrous. Leaves 1 or 2, basal, filiform, about as wide as the culms, the lower reduced to a bladeless sheath or a sheath bearing merely an involute appendage, the upper with blade up to ⅓ as long as the culm, or reduced like the lower one; stomata paracytic; chlorenchyma radiate; the bundle sheaths 2-layered ("*Cyperus* type"). Inflorescences unbranched, a sessile cluster of 1–4 dense spikes; bracts 1–4, filiform, 1–4 times as long as the spikes, leaflike, the longest erect, appearing as a continuation of the culm, the other(s) shorter than or equaling the spikes, borne approximately perpendicular to the culm; rays none. Spikes ("spikelets") 1–4, sessile, ovoid [globose]; denuded rachis persistent, with rhombic scars where the spikelets were attached. Spikelets ("flowers") [20–]50–150, densely spirally arranged, borne approximately perpendicular to the rachis, deciduous. Scales (1, 2, or) 3; outer scale lanceolate to ovate-lanceolate, planar or nearly so, with 2 conspicuous medial veins and a less conspicuous central one, laterally weakly 1- or 2-nerved or essentially nerveless, mucronulate [aristate]; inner scale hyaline, equaling or shorter than the outer, or reduced to a scalelike appendage much shorter than the outer, with 3–5 inconspicuous veins or veinless, or absent; third scale present between the outer scale and the achene in some species, similar to or smaller than the second. Flowers perfect. Perianth lacking. Stamens 1 or 2; filaments capillary, about ¾ as long as the outer scale; anthers ovoid, the apices of the connectives not prolonged; pollen grains 4-aperturate, obovoid to subspheroidal, psilate or scabrate. Styles filiform; stigmas 2, about ½ as long as the styles, minutely swollen apically, glabrous, deciduous before the achenes mature. Achenes trigonous to terete, obovoid to cylindrical, slightly shorter than the outer scale, the base sessile to stipitate, the apex obtuse to subtruncate, apiculate, the surface papillose. Embryos ellipsoid. Base chromosome number 6. (Incl. *Ascolepis* Nees ex Steudel, *Hemicarpha* Nees ex Arnott.[18]) TYPE SPECIES: *L. senegalensis* (Lam.) T. & H. Durand (*L. argenteum* (Vahl) R. Br., *nom. illeg.*; see Haines & Lye). (Name from Greek, *lipo,* to fall, and *carpha,* chaff, referring to the deciduous hyaline inner scale of the spikelet.)

A genus of about eight species occurring in tropical and warm-temperate regions. Five grow in North America: *Lipocarpha maculata* (Michx.) Torrey, on the Coastal Plain from Virginia to Texas, southward into the tropics; *L. occidentalis,* restricted to the Pacific coast; *L. Drummondii,* from Oklahoma and Texas west to New Mexico; *L. aristulata,* across the United States from South Carolina and Florida west to Washington and California; and *L. mi-*

[18]The inclusion of *Hemicarpha* in *Lipocarpha* necessitates the following new combinations for species occurring in the New World:

Lipocarpha aristulata (Cov.) G. Tucker, based on *Hemicarpha micrantha* var. *aristulata* Cov. Bull. Torrey Club **21:** 36. 1894.

L. Drummondii (Nees) G. Tucker, based on *Hemicarpha Drummondii* Nees in Martius, Fl. Brasil. **2**(1): 62. 1842.

L. micrantha (Vahl) G. Tucker, based on *Scirpus micranthus* Vahl, Enum. **2:** 254. 1806.

L. occidentalis (Gray) G. Tucker, based on *Hemicarpha occidentalis* Gray, Proc. Am. Acad. **7:** 391. 1868.

L. Schomburgkii (Friedl.) G. Tucker, based on *Hemicarpha Schomburgkii* Friedl. Am. Jour. Bot. **28:** 860. 1941.

crantha, throughout the United States and southeastern Canada, southward to tropical South America. *Lipocarpha Schomburgkii* is known only from the Guyana region of northern South America.

All species are small, inconspicuous plants of disturbed wet soils, especially shores of ponds and pools. Because of their small size (less than 30 cm tall, and often less than 1 cm!), they are easily overlooked and are probably more frequent and widely distributed than available collections indicate.

Raynal's view that *Lipocarpha* is a highly reduced derivative of *Cyperus* seems well founded and is accepted here. The fact that both genera have "*Cyperus*-type" kranz anatomy (Metcalfe) further strengthens this conclusion. The achene and subtending scales of *Hemicarpha* are probably homologous to a single spikelet of *Kyllinga* or *Cyperus.* Friedland suggested that the inner hyaline scale represented five perianth members that correspond to the bristles subtending the achenes in some species of *Scirpus.* Raynal's interpretation of the inner scales of *Lipocarpha* (and *Hemicarpha*) as reduced scales of a spikelet appears more plausible than Friedland's view.

Haines & Lye studied the African species previously assigned to *Hemicarpha* and *Lipocarpha* and concluded that the two genera should perhaps be merged. Goetghebeur (pers. comm.) has recently studied all the Old World species of these genera, as well as those of the closely related genus *Ascolepis.* He concluded, as I had from my independent investigations, that the three genera should be combined.

Chromosome numbers have been reported for *Lipocarpha argentea* R. Br. ($2n = 26$) and *L. microcephala* Kunth ($2n = 46$). This suggests a base chromosome number of 6.

No species is gathered as food or for medicinal purposes. *Lipocarpha argentea* and *L. microcephala* (R. Br.) Kunth are recorded as weeds in eastern Asia (Holm *et al.*).

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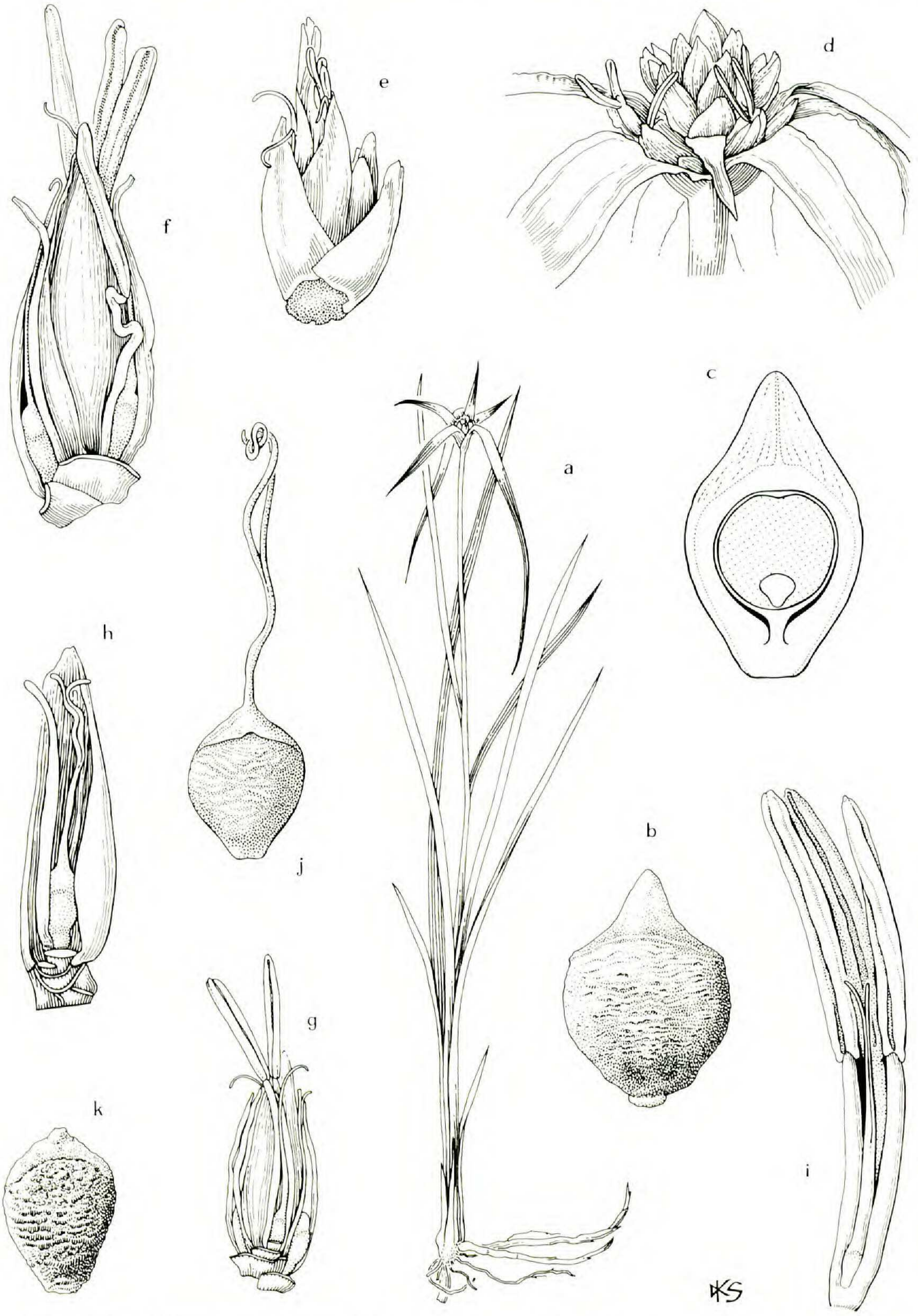

FIGURE 3. *Rhynchospora* sect. DICHROMENA. a–c, *R. colorata:* a, habit (note rhizomes to right), × ½; b, mature achene, tubercle scarcely decurrent on body of achene, × 20; c, same, in longitudinal section, the 2 layers of the achene wall separated by dotted line, seed coat unshaded, endosperm stippled, embryo unshaded, × 20. d–k, *R. floridensis:* d, head of spikelets subtended by involucral bracts, × 3; e, 1 large and 1 small spikelet enclosed by 2 scales, × 6; f, abaxial surface of spikelet, 2 scales removed, flowers protandrous, × 10; g, same spikelet, adaxial surface, 1 stamen and 3 scales removed, × 6;

Tribe SCHOENEAE Dumortier, Fl. Belg. 144. 1827. (Tribe Rhynchosporeae Fenzl in Endlicher, Gen. Pl. **2:** 115. 1836.)

11. **Rhynchospora** Vahl, Enum. Pl. **2:** 229. 1806, *nom. cons.*

Small to large, caespitose or single-stemmed, perennial [annual] herbs of moist open woods, bogs, pocosins, ditches, and pond shores. Roots fibrous; rhizomes or stolons present in a few species. Culms trigonous, subtrigonous, or terete, smooth throughout or ribbed just below the inflorescence, glabrous, leafy [leafless]. Leaves numerous, basal, cauline, or both; basal leaves with blades flat to conduplicate or involute-filiform, the margins and midveins generally scabrellate with unicellular [multicellular] prickles, the surfaces glabrous or with prickles like those on the margins, or pubescent with long, flexible, unicellular hairs, or papillose (in *R. alba*); cauline leaves shorter than but otherwise similar to the basal ones; stomata paracytic, generally confined to the abaxial surface; chlorenchyma not radiate [radiate in some tropical species]. Inflorescences terminal (sometimes also lateral, the lateral ones smaller and less branched than the terminal), fasciculate or cymose; bracts 1–6, leaflike (sometimes basally whitened); rays slender, terete, smooth or scabrellate; heads loosely to densely ovoid or capitate. Spikelets solitary, globose, ellipsoid, or slenderly lanceolate, the 1–5 basal scales sterile. Scales spirally arranged, closely imbricate, ovate to lanceolate, entire or mucronulate at apex, nerveless to rather prominently nerved, the midvein most conspicuous. Flowers perfect (the terminal 1 or 2 scales sterile or subtending rudimentary ovaries and functional stamens). Perianth bristles lacking or 1–6(–20), smooth, barbed, or plumose, persistent. Stamens (1–)3(–12); filaments capillary or ribbonlike; anthers elliptic to oblong, the apices of the connectives not prolonged; pollen grains uniaperturate, obovoid, psilate or scabrate, binucleate. Styles glabrous; the stigmas longer than, equaling, or much shorter than the style. Achenes lenticular (dorsiventrally flattened), ovoid to slenderly ellipsoid, crowned with a pyramidal to subulate tubercle shorter than to 3 times longer than the body of the achene, the base sessile to conspicuously stipitate, the lateral edges often raised to form a conspicuous ridged margin, the surface alveolate to cancellate (rarely smooth or nearly so), transversely rugulose or not. Base chromosome number 5. (Incl. *Psilocarya* Torrey, *Dichromena* Pers., *Calyptrostylis* Nees.) TYPE SPECIES: *R. alba* (L.) Vahl (*Schoenus albus* L.), *typ. cons.* (Name from Greek, *rhynchos,* snout, and *spora,* seed, in reference to the prominently beaked achenes.)

A genus of about 225 species, worldwide in distribution, with greatest diversity in the New World tropics; about 60 occur in the southeastern United States. Temperate North America, especially the southeastern Coastal Plain, is rich in species, and there are many others in the Old World tropics. Only a

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h, flower with subtending scale, anthers fallen, 5 scales and rachilla of spikelet removed, × 10; i, flower removed from spikelet, anthers dehiscing, styles not yet elongated, stigmas not receptive, × 12; j, nearly mature achene with persistent style and stigmas, × 20; k, mature achene, tubercle decurrent on body of achene, × 20.

few species are indigenous to temperate Eurasia—three species in Europe and four in the Soviet Union east of the Urals.

Kükenthal's worldwide monograph (1949, 1950, 1951) provided a basis for identification and further study of the genus *Rhynchospora*. Gale, in her careful, well-illustrated monograph, did much to clarify the taxonomy of the North American species. Thomas (1984) has recently investigated the tropical section DICHROMENA (Pers.) Pfeiffer and confirmed its inclusion in *Rhynchospora*.

The genus is little known cytologically; chromosome numbers have been published for only ten species (summarized by Thomas, 1984). These suggest a base chromosome number of 5, in keeping with the base number for other genera of the family.

There are three subgenera in *Rhynchospora* (Kükenthal, 1949, 1950, 1951). The largest of these, including about 54 of the 60 species in our area, is subg. RHYNCHOSPORA (*Eurhynchosporae* Gray), species of which have papery spikelet scales and stigmas equaling or longer than the styles. Complete descriptions of the southeastern species were provided by Gale.

Species of sect. DICHROMENA have sessile capitate inflorescences and whitish spikelets often subtended by whitish bracts and lack perianth bristles. The section is primarily neotropical in distribution and contains 23 species, of which four are present in the United States. Three occur in the Southeast. Insect pollination has evolved in plants of this section, as was first noted in 1893 by De Lagerheim and later studied by Uphof and Leppik.

Thomas (1984) reviewed previous investigations of entomophily in species of sect. DICHROMENA and made thorough field and laboratory studies. Fifteen species of bees (Hymenoptera) visit flowers of plants included in this section. The bees exhibit constancy, visiting four to ten inflorescences in a population before leaving. The flowers have no fragrance and no nectar; the white color of the bracts and spikelets attracts the bees, and pollen is the only reward. The pollen grains have a sticky "pollenkit"; thus, they aggregate and stick to the bee's body and legs. There is probably some transfer of pollen by the wind. All species of sect. DICHROMENA are self-compatible. Thomas (1984) postulated that the evolution of entomophily may have permitted the species to radiate into shaded tropical forests, where a lack of air movement necessary for wind pollination is compensated for by insect and self-pollination.

No species of *Rhynchospora* is gathered for food or medicinal uses. Several species are detrimental weeds in rice fields, both in the Old World and in the southeastern United States.

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12. **Dulichium** Persoon, Syn. Pl. **1:** 65. 1805.

Perennial herbs of swamps, fens, and shores. Roots fibrous; rhizomes horizontal. Culms 1–3, terete, hollow, glabrous. Basal leaves bladeless; sheaths appressed; cauline leaves several, the blades lanceolate, about 1–2 times longer

than the sheaths, auriculate, planar, with margins and midveins densely scabrellate abaxially; stomata confined to the adaxial surfaces (sometimes a few present near the margins on the abaxial surface); chlorenchyma not radiate; air cavities present. Inflorescences solitary in the axils of the upper leaves; rays and rachises slender, compressed, scabrellate on the edges; spikes loosely ovoid, appearing flattened from the distichous arrangement of the spikelets. Spikelets 3–20, linear-lanceolate, flattened; rachilla persistent, the internodes with hyaline margins, the lowermost scale sterile (except in the terminal spikelet). Scales 3–9, deciduous as the achenes mature, lanceolate, conduplicate, acute, 5- to 9-nerved, the midveins scabrellate. Flowers perfect. Perianth bristles 6–9, 1–2 times as long as the mature achene, retrorsely barbed. Stamens 3; filaments ribbonlike, nearly as long as the scales; anthers linear, the apices of the connectives minute. Style capillary, glabrous; stigmas 2, about as long as the style, glandular-pubescent. Achenes planoconvex, narrowly ellipsoid, the apex acute, the base stipitate, the surface puncticulate. Embryos turbinate. Base chromosome number 16. TYPE SPECIES: *D. arundinaceum* (L.) Britton. (Name from the Greek *duo,* two, and *leichon,* scale, referring to the two-ranked scales of the spikelets.)

A monotypic genus of wetland plants endemic to temperate North America. *Dulichium* is easily distinguished from other Cyperaceae by its characteristic distichous spikelet scales and its three-ranked cauline leaves. An interesting, apparently uninvestigated feature of the plants is that in adjacent culms arising from the same rhizome, the leaves are spiraled clockwise in one and counterclockwise in the next. The single species, *D. arundinaceum,* is distributed from Newfoundland to southeastern Manitoba, south to southern Florida and eastern Texas, and disjunctively in the area from northwestern Montana and southwestern British Columbia south, mostly west of the Cascades and the Sierra Nevada, to central California (Wood, 1972, *map*). The genus had a wider distribution during the Pleistocene when it occurred in Europe (Wood, 1971, *map*). Fossils of this species are known from the Pliocene in the Soviet Union (Daghlian). Infraspecific variation in fossil achenes from Europe has been studied by Truchanowiczowna.

Dulichium has usually been placed in the tribe Cypereae, near *Cyperus.* Linnaeus (Sp. Pl. **1:** 45. 1753) included the species in *Cyperus,* presumably because of its distichous spikelet scales. The two genera differ, however, in several important features: *Dulichium* has widely spaced axillary inflorescences subtended by leaflike bracts with conspicuous sheaths, while *Cyperus* has apically clustered inflorescence branches subtended by sheathless bracts; *Dulichium* has one sterile scale at the base of each spikelet, and *Cyperus* has two; *Dulichium* has perianth bristles, but *Cyperus* does not.

The embryos of *Dulichium* resemble those found in *Rhynchospora,* rather than those of any genus of the Cypereae (Van der Veken). A new monotypic tribe, the Dulichieae, has recently been proposed for this genus by Schulze-Motel (1959).

Plants of this genus have been neither reported to have economic use nor noted as weeds.

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13. **Schoenus** Linnaeus, Sp. Pl. 42. 1753; Gen. Pl. ed. 5. 26. 1754.

Caespitose perennials of open sunny wetlands. Rhizomes short, oblique. Culms terete, hollow, glabrous. Leaves all basal; sheaths tough, glossy, glabrous, ligule lacking; blades linear, subcylindrical, upper surface flat or broadly convex; stomata paracytic, on both surfaces [mostly adaxial]; chlorenchyma not radiate. Inflorescences terminal, sessile, capitate [diffusely branched]; bracts 1 or 2, oblique to erect, sheathless or essentially so, basally expanded and partly clasping the spikelets, distally linear; rays lacking. Spikelets (1–)10–25, oblong-ellipsoid, flattened, the 2 or 3 basal scales sterile; rachilla wingless, more or less deciduous at maturity. Scales distichous, 3–8, oblong, acute but not mucronate, distally scabrellate, laterally nerveless, medially 1-nerved. Flowers perfect. Perianth bristles lacking to 6, smooth or scabrellate. Stamens 3; filaments ribbonlike; anthers linear, the apices of the connectives subulate, conspicuous; pollen grains 4-porate, obovoid, finely scabrate (pore areas frustillate). Styles trigonous to subtrigonous, glandular; stigmas 3, capillary, shorter than the styles, glandular. Achenes roundly trigonous to subterete, ovoid to ellipsoid, the apex broadly rounded, the base gradually tapered to a stipe, the surface smooth or barely reticulate, glossy. Base chromosome number 20(?). TYPE SPECIES: *S. nigricans* L.; see Britton & Millspaugh, Bahama Fl. 56. 1920. (Name from Greek *schoinos,* for a rushlike plant.)—BLACK-HEADED SEDGE.

A genus of about 80 species, mostly restricted to Australasia but with a few occurring in Africa, Eurasia, and the New World. *Schoenus nigricans* L., $2n = 54, 55$, is present in North America. It is common in southern Florida but rare in the Florida Panhandle, where it grows in wet grasslands over limestone outcrops; it also occurs in the southwestern United States in the mountains and valleys of western Texas, southern California, and southwestern Nevada, where it grows in marshes and thermal springs. It is also reported from the West Indies, Europe, and Asia.

Kükenthal published a worldwide revision of *Schoenus,* and the genus has received little subsequent systematic attention. The European species have been investigated ecologically. *Schoenus nigricans* requires aluminum ions for growth, and its range in the blanket bogs of the British Isles is thus limited to the coastal region of western Ireland.

Plants of the genus have little economic significance. Wet meadows dominated by *Schoenus ferrugineus* L. are mowed for fodder in northern and central Europe. The species is adapted to low nutrient levels and is quickly displaced by grasses when fertilizers are regularly applied.

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14. **Cladium** P. Browne, Civ. Nat. Hist. Jamaica, 114. 1756.

Stoloniferous, single-stemmed or loosely clustered, medium to large perennials of sunny wetlands. Culms terete, roundly trigonous, or thickly crescentiform, hollow, glabrous. Leaves all cauline; sheaths glabrous, much shorter than the blades; blades flat or slightly conduplicate to subinvolute, the margins and midveins sparsely scabrellate to harshly scabrous; chlorenchyma not radiate; alternate bundles inverted. Inflorescences pedunculate, terminal or both lateral and terminal, diffusely branched; bracts leaflike but with shorter blades; primary rays terete, wirelike and slightly drooping, glabrous; secondary rays similar to primary but shorter and more slender; tertiary and quaternary rays regularly produced in some species, these subtended by lanceolate scalelike bracts and sheathing prophylls (involucels). Spikelets in glomerules of 1–5, narrowly ellipsoid to lanceolate; rachilla wingless. Scales 3–5, the basal 1–3 sterile, ovate to oblong-lanceolate. Flowers perfect or imperfect (the distal flower of a spikelet perfect, the subdistal staminate). Perianth lacking. Stamens 2 or 3; filaments about as long as the subtending scale, flattened; anthers linear, the apices of the connectives subulate; pollen grains 4-porate, narrowly obovoid (sometimes with a peculiar apical appendage containing the degenerate nuclei), scabrate. Styles subtrigonous, glabrous; stigmas 3, longer than the styles, glan-

dular. Achenes terete, ovoid, the apex broadly round (the withered style base sometimes persistent), the base truncate and impressed, sometimes stipitate, the surface smooth or nearly so. Embryos small, broadly obovoid, scarcely differentiated (the first leaf not developed). Base chromosome number 20. TYPE SPECIES: *C. Mariscus* (L.) Pohl (*Schoenus Mariscus* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 347. 1913). (Name from Greek *clados,* branch, referring to the highly branched inflorescences.)—TWIG-RUSH, SAW-GRASS.

Cladium is here accepted in the strict sense—i.e., consisting of three species: *C. Mariscus, C. mariscoides* (Muhl.) Torrey, and *C. jamaicense* Crantz. Kükenthal treated the genus more broadly, including *Machaerina* Vahl. Recent studies by Vanhecke and Metcalfe argue against such a broad circumscription. Species of *Cladium* consistently differ from those of *Machaerina* in their smaller, less differentiated embryos and their isobilateral leaves with inverted bundles (illustrated by Metcalfe).

Two species occur in our area. *Cladium jamaicense,* the saw-grass of the Florida Everglades, grows in tidal marshes and coastal wetlands from eastern Virginia to Mexico and the West Indies. Some authors (Kükenthal, Raynal) included *C. jamaicense* in the European *C. Mariscus*; Kern also included the Australasian *C. procerus* S. T. Blake. The second species in our area, *C. mariscoides,* occurs in brackish wetlands and inland fens and marshes from Newfoundland to Saskatchewan to Florida and Missouri; it is rare in the Southeast. Raynal, without discussion, treated *C. mariscoides* and *C. jamaicense* as synonyms of *C. Mariscus,* an extreme view not followed by anyone else.

Cladium jamaicense is important as the dominant species of much of the Florida Everglades. The culms and leaves of *C. Mariscus* are gathered and used in the manufacture of paper products in the Danube Delta, Romania.

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Tribe SCLERIAE Kunth ex Fenzl in Endlicher, Gen. Pl. **2:** 114. 1836.

15. **Scleria** Bergius, Sv. Vet.-akad. Handl. **26:** 142. 1765.

Small to medium, erect [scandent], perennial or annual herbs of grasslands, open woods, fens, and shores. Roots fibrous; rhizomes regularly present in many species, indurate, sometimes tuberlike, simple or branched. Culms trigonous, glabrous, pubescent, or scabrellate [retrorsely scabrous], sometimes bulbous basally. Basal leaves bladeless or nearly so. Cauline leaves several; sheaths 3-angled, glabrous or more often scabrellate or pubescent; blades lanceolate to linear or filiform, flat to slightly conduplicate [involute or thickened], glabrous, scabrellate, or pubescent; chlorenchyma not radiate. Inflorescences paniculate, 1 to several, terminal or lateral and terminal; bracts leaflike but shorter than or equaling the cauline leaves; rays trigonous, scabrellate on the angles or smooth, secondary rays regularly produced in some species. Spikelets 1–6, lanceolate to linear or oblong. Scales 1–6, ovate-deltoid, acute, mucronulate to cuspidate, conspicuously medially 1-nerved, laterally nerveless, glabrous or pubescent. Flowers imperfect; carpellate flower(s) 1 (or 2), borne at the base of the spikelets or in separate spikelets. Perianth bristles lacking. Stamens 1–3; filaments capillary; anthers narrowly ellipsoid to linear, the apices of the connectives frequently prolonged as slender, subulate, reddish appendages; pollen grains uniaperturate, obovoid to subspheroid, psilate. Hypogynium, if present, pebbled or warty, entire or with 3 acute to obtuse [truncate or acuminate], ciliate or glabrous lobes clasping the base of the achene. Styles slender, glandular; stigmas 3, capillary, shorter than the styles. Achenes roundly trigonous to terete, globose to ellipsoid, the apex broadly rounded (sometimes apiculate), the base sessile to broadly stipitate, the surface smooth, reticulate, trabeculate, rugose, glabrous, or pubescent. Base chromosome number 7(?). TYPE SPECIES: *S. flagellum-nigrorum* Berg.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 348. 1913. (Name from Greek *skleros,* harsh, the culms of the type species being bound together into whips for beating slaves in Surinam; often incorrectly said to be derived from Greek *skleria,* tough, in reference to the achene walls; see Holm, 1898).—NUT-RUSH.

A predominantly tropical genus of some 200 to 225 species. Centers of diversity are tropical South America, tropical Africa, and southeastern Asia. Twelve species occur in the United States, all east of the Great Plains. All are present in the Southeast. Several range northward into northeastern North America, reaching Massachusetts, southern Ontario, and southern Minnesota. Two of our representatives occur southward into the West Indies. Many of our species are endemic, as are most other taxa of *Scleria.* Many African species, for example, occur only in Africa, and several are restricted to a single country or are known from only one collection. Such endemism contrasts with the distribution of the other large, mostly tropical genera of the family, such as *Cyperus,* in which about one-fifth of the species are pantropic. Only two species of *Scleria, C. lithosperma* (L.) Sw. and *S. hirtella* Sw., are reported from both the Old World and the New.

The morphology of the achenes and the hypogynia has traditionally provided the chief criteria for the circumscription of species. Core noted that some species—for example, the South American *Scleria leptostachya* Kunth—produced both smooth and verrucose achenes, sometimes within a single collection and sometimes within the same inflorescence. Nelmes (1955, 1956) reported similar problems with certain African species, and he relied on features of the rhizomes, ligules, and inflorescence (in addition to achene morphology) in his classification of the African species. The hypogynium is apparently derived from receptacular tissue, as is shown by its vascularization (Blaser, 1940, 1941b).

Robinson (1966) indicated that many of the southern African species of *Scleria* are strong calcicoles. This autecology contrasts with that of the American species, most of which grow in acidic coastal plain habitats. Apparently only one American species, *S. nitida* Willd. (which Fairey treated as a synonym of *S. verticillata*) is a calciphile (Fernald).

Core recognized five sections in the genus, of which two, sects. SCLERIA (sect. *Euscleria* Endl.) and HYPOPORUM (Nees) Endl., are represented in the Southeast. In sect. HYPOPORUM the species have androgynecandrous spikelets (carpellate flowers below the staminate) and lack hypogynia. There are five species in our area: *S. verticillata* Willd., *S. hirtella* Sw., *S. Baldwinii* (Torrey) Steudel, *S. georgiana* Core, and *S. lithosperma* (L.) Sw. Species of sect. SCLERIA have unisexual spikelets and three-lobed, entire hypogynia. In our area this section includes seven species: *S. triglomerata* Michx., *S. minor* Stone, *S. oligantha* Michx., *S. ciliata* Michx., *S. pauciflora* Willd., *S. Curtissii* Britton, and *S. reticularis* Michx.

The genus is scarcely known cytologically. Reports are available only for *Scleria tesselata,* $2n = 28$, of southeastern Asia. This suggests the base number $x = 7$ for the genus.

Species of *Scleria* have unusual embryological features (Nijalingappa). In *S. foliosa* A. Rich. the embryos have both chalazal and micropylar haustoria. Wall formation in the endosperm is complete in the Cyperaceae, except in *Scleria,* where it is incomplete. The surface of the cotyledon is papillose in *Scleria* but smooth in other genera of the family.

Robinson (1966) stated that several southern African species had "citrus-scented" foliage; in fact, he used this as a lead characteristic in his key. Thus, further investigation of the chemistry of these plants might be fruitful.

The fruits of *Scleria triglomerata* are dispersed by ants. The hypogynium functions as an elaiosome (Gaddy). However, Robinson (1962) suggested that the hypogynium provided buoyancy for the achenes of several southern African species and was thus an adaptation for dispersal along water channels that might later provide appropriate conditions for germination and growth of seedlings.

No species of *Scleria* is gathered for food. Rhizomes of *S. hirtella* have been employed medicinally in Colombia (Core). The tough, scabrous foliage of *Scleria* is unsuitable for cattle forage. About ten species are noted as significant weeds in Central and South America, tropical Africa, and southeastern Asia. *Scleria sumatrensis* Retz. is a detrimental weed in Borneo (Holm *et al.*).

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Tribe CARICEAE Kunth ex Dumortier, Fl. Belg. 144. 1827.

16. **Cymophyllus** Mackenzie in Britton & Brown, Illus. Fl. No. U. S. Can. ed. 2. **1:** 441. 1913.

Loosely caespitose perennials of mesic montane forests. Rhizomes oblique. Culms subterete, smooth, aphyllopodic. Leaves several; lowest with papery sheath only, bladeless; uppermost sheathless, the blade broadly lanceolate, broadly rounded at apex, undulate at margins (especially so when dried), conspicuously multinerved but lacking a differentiated midvein and ligule. Inflorescences single densely ellipsoid spikes, 1 per culm, terminal, with the pistillate flowers below the staminate; bracts single broadly deltoid entire scales, 1 per

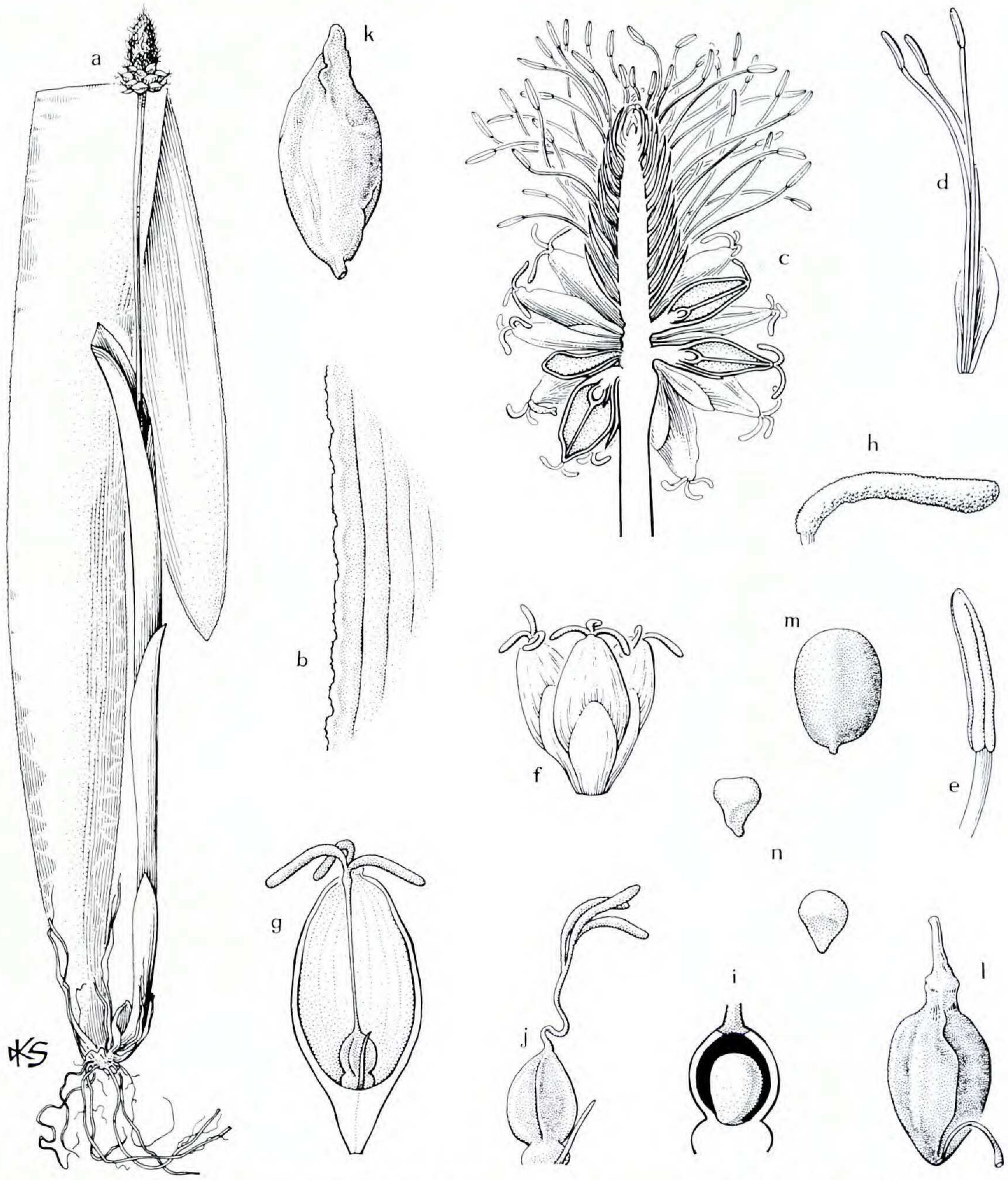

FIGURE 4. *Cymophyllus.* a–n, *C. Fraseri:* a, habit (portion of plant, leaf of preceding season, plus new shoot terminated by inflorescence just past anthesis), × ½; b, detail of undulate leaf margin, × 6; c, longitudinal section of inflorescence, staminate flowers above, carpellate below, × 2; d, staminate flower with subtending scale, × 3; e, anther (basifixed), × 12; f, 3 carpellate flowers enclosed in perigynia, each in axil of a scale, × 3; g, longitudinal section of perigynium to show carpellate flower (note bristlelike rachilla), × 5; h, stigma (note lack of papillae—species is insect pollinated), × 12; i, longitudinal section of gynoecium to show single basal anatropous ovule, × 12; j, early stage of developing fruit, growth of gynoecium producing kink in style, × 5; k, perigynium enclosing mature achene, × 6; l, immature achene (note rachilla at base), × 6; m, achene, × 6; n, embryo, dissected from base of achene, 2 views, × 25.

spike, broader than but otherwise like the pistillate scales immediately above it. Flowers imperfect. Perianth lacking. Scales oblong-ovate, entire, without conspicuous midvein or nerves. Stamens 3; filaments slender, 1–3 times as long as the subtending scales; anthers slenderly ellipsoid, the connectives not

prolonged. Perigynia 10–30, broadly ellipsoid, roundly trigonous, abruptly contracted to a short, entire beak, weakly 20- to 30-nerved, glabrous; rachilla filiform, ⅓–½ as long as the perigynium. Styles slender; stigmas 3, slightly longer than the style, exserted from the beak of the perigynium. Achenes trigonous, broadly ellipsoid, the apex broadly rounded, the base abruptly stipitate, the surface smooth, glossy. Chromosome number unknown. TYPE SPECIES: *C. Fraseri* (Andrews) Mackenzie (*Carex Fraseri* Andrews; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1**: 441. 1913.) (Name from Greek *kuma,* wave, and *phyllon,* leaf, in reference to the undulate margins of the leaves.) —FRASER'S SEDGE.

A monotypic genus endemic to the southern Appalachians. The sole species, *Cymophyllus Fraseri,* is well known for its attractive white spikes that are conspicuous when the plants flower in the spring. The plants grow in mesic to somewhat damp soils in mixed hardwood forests, particularly on northern and western slopes at middle elevations. The species is known from eastern Tennessee and northwestern South Carolina, north through the Ridge and Valley and Blue Ridge provinces to extreme south-central Pennsylvania (Somerset County). Clarkson listed known collections arranged by state and county.

The systematic position of the genus has been disputed. Kükenthal treated the species as *Carex Fraseri* (sect. *Leucocephali* Holm of subg. *Primocarex* Kükenthal). Mackenzie, Fernald, Metcalfe, and Reznicek (pers. comm.) recognized *Cymophyllus* as a distinct genus. The conspicuous white inflorescences of *C. Fraseri,* while unique among North American species of the tribe Cariceae, are also known in at least one Old World species of *Carex* (*C. baldensis* L.). White inflorescences are associated with insect pollination (discussed below) and have evolved in *Cyperus* and *Rhynchospora.* In *C. Fraseri* there is a rachilla within the perigynium. While a rachilla is not present in any temperate North American species of *Carex,* it does occur in several other species (e.g., *C. microglochin* Wahlenb. (boreal North America, cold-temperate Eurasia, southern South America, *fide* Fernald)). Anatomical evidence (summarized by Metcalfe) gives the strongest support for the generic status of *Cymophyllus.* In *Cymophyllus Fraseri* the culms are terete (trigonous (rarely hexagonal) in *Carex*); the leaves lack ligules (which are always present in *Carex*); the uppermost leaf lacks a sheath and consists of blade only (sheaths are always present in the cauline leaves of *Carex*); the large leaf blade is broadly rounded apically (acute in *Carex*) and lacks the differentiated midrib and the adaxial layer of bulliform cells typical of *Carex* (Holm; Metcalfe). In *Cymophyllus Fraseri* the median vascular bundle has an incomplete adaxial sclerenchyma cap, and there is an abaxial sclerenchyma girder (Metcalfe). The presence of perigynia in *Carex* and *Cymophyllus* clearly indicates that they are closely related, although it is unclear how. The presence of a rachilla in *Cymophyllus* suggests that this genus might be closer to the Southern Hemisphere *Uncinia* Pers. than to *Carex.*

Cymophyllus Fraseri has long been suspected of being entomophilous (Clarkson), although there has been only a single field study documenting entomophily (Thomas). Four bee and one fly species were observed to visit spikes of this species, which flowers from late April to mid-June. The insects collect pollen

for food and transfer it from plant to plant. They land on the lower, relatively broad carpellate portion of the spikes, where they deposit pollen on the stigmas. They then crawl up to the anthers, collect pollen, and fly to another inflorescence. The pattern of stigmas first, then anthers, probably enhances outcrossing (Thomas).

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17. **Carex** Linnaeus, Sp. Pl. **2:** 972. 1753; Gen. Pl. 280. 1754.

Caespitose or single-stemmed, small to medium-sized perennials of wet to dry woods, grasslands, rock outcrops, pocosins, fens, bogs, marshes, and swamps. Roots fibrous, smooth or pubescent; rhizomes (infrequently lacking) short and oblique or long and horizontal, with closely appressed, lanceolate scales. Culms loosely to densely clustered or solitary, fertile or both vegetative and fertile, trigonous [hexagonal], the angles smooth or scabrellate. Basal leaves several to many; sheaths smooth; ligule hyaline, glabrous; blades flat, conduplicate, plicate, or involute, scabrellate (or smooth) on margins and midveins, sometimes microscopically papillate on 1 or both surfaces, infrequently glaucous; stomata paracytic, present on one or both surfaces; chlorenchyma not radiate; air chambers frequently present; cauline leaves similar to basal ones but shorter and fewer, sometimes lacking. Inflorescences simple or compound, monoecious (rarely dioecious); bracts lacking or 1–6; spikes 1 to several, loosely to densely ovoid to slenderly cylindrical, sessile or borne on simple [branched] erect to pendent peduncles; each spike subtended by a leaflike or filiform basal bract; spikes wholly carpellate or wholly staminate or gynecandrous or androgynous.

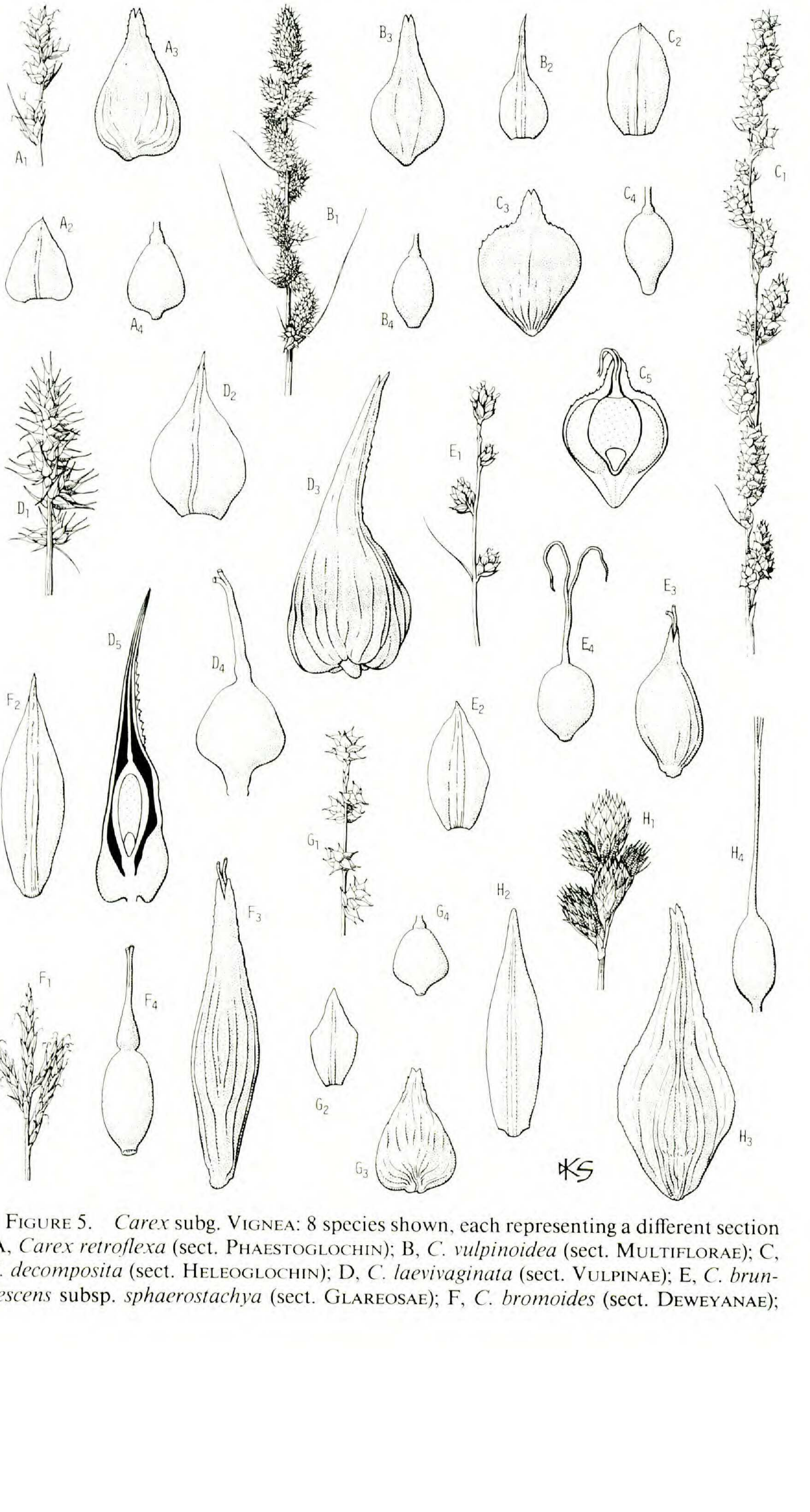

FIGURE 5. *Carex* subg. VIGNEA: 8 species shown, each representing a different section (A, *Carex retroflexa* (sect. PHAESTOGLOCHIN); B, *C. vulpinoidea* (sect. MULTIFLORAE); C, *C. decomposita* (sect. HELEOGLOCHIN); D, *C. laevivaginata* (sect. VULPINAE); E, *C. brunnescens* subsp. *sphaerostachya* (sect. GLAREOSAE); F, *C. bromoides* (sect. DEWEYANAE);

Staminate scales lanceolate (the margins rarely fused basally), hyaline to chartaceous, 1- (to 3-)nerved; carpellate scales lanceolate to broadly ovate, chartaceous, 1- (to 3-)nerved. Flowers imperfect, protogynous or protandrous. Perianth lacking. Stamens 3; filaments capillary or ribbonlike, longer than the subtending scales; anthers broadly to slenderly ellipsoid; pollen grains 1- or 4-aperturate, obovoid or subspheroidal, psilate, trinucleate. Perigynia solitary in the axils of carpellate scales, lenticular, subterete, trigonous, or slightly to strongly compressed (beak, when present, less than to equaling or sometimes longer than the body), coriaceous to chartaceous, the faces nerveless or with 1–15 nerves, minutely papillose or not, scabrellate or essentially smooth, dull or glossy. Styles capillary, straight or curved; stigmas 2 or 3 [or 4], equaling or exceeding the styles in length, smooth, papillose, or glandular, at anthesis exserted through the orifice of the perigynia. Achenes lenticular or trigonous [4-sided], ovoid to ellipsoid, ¼ as long as to nearly as long as the body of the perigynium, sessile or stipitate, apiculate or entire, the faces flat, convex, or concave, the edges obtuse or acute (invaginate in a few species), the epidermal cells translucent, opaque, or glossy. Embryos obconical, the radicle basal. Base chromosome number 5. TYPE SPECIES: *C. hirta* L., not *C. pulicaris* L.; see Hitchcock & Green, Prop. Brit. Bot. 187. 1929, and comments by Voss, Mich. Bot. **11:** 31, 32. 1972. (The classical Latin name, perhaps derived from the Greek *keirein,* to cut, due to the sharp margins and keels of the leaf blades.) —SEDGE.

A very large, cosmopolitan genus, reported to contain from 1000 to 2000 or even 2500 species (Standley, 1985a), including 165 that occur in the Southeast. Four subgenera have been recognized, of which two are represented in the United States. Subgenus INDOCAREX Baillon (inflorescences richly branched, branches subtended by tubular prophylls) comprises about 50 species of the Old World tropics. Subgenus VIGNEA (Lestib.) Kükenthal (spikes all either gynecandrous or androgynous, sessile, stigmas two, perigynia and achenes lenticular) includes about 500 species; it is worldwide in distribution but is most diverse in the northern temperate and boreal regions. Subgenus CAREX (subg. *Eucarex*; spikes sessile or pedunculate, some exclusively staminate or pistillate, stigmas 3 (rarely 2), perigynia and achenes trigonous) is the largest subgenus, with about 800 species. Subgenus PRIMOCAREX Kükenthal (spikes solitary, terminal, stigmas 2 or 3, achenes lenticular or trigonous) is not represented in our area.

The evolution of the tribe Cariceae is largely unclear. Due to shared features of the inflorescences, Smith & Faulkner suggested that it arose from ancestors akin to the Scleriae or the Hypolytreae. Kukkonen (1963), because of similar

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G, *C. Howei* (sect. STELLULATAE); H, *C. scoparia* (sect. OVALES)). Four or 5 items illustrated for each, these drawn at same magnification throughout: 1, inflorescence, × 1; 2, scale subtending perigynium, abaxial surface, × 10; 3, mature perigynium, abaxial surface, × 10; 4, mature achene, abaxial surface, × 10; 5, longitudinal section of mature perigynium and achene (C and D only), × 10.

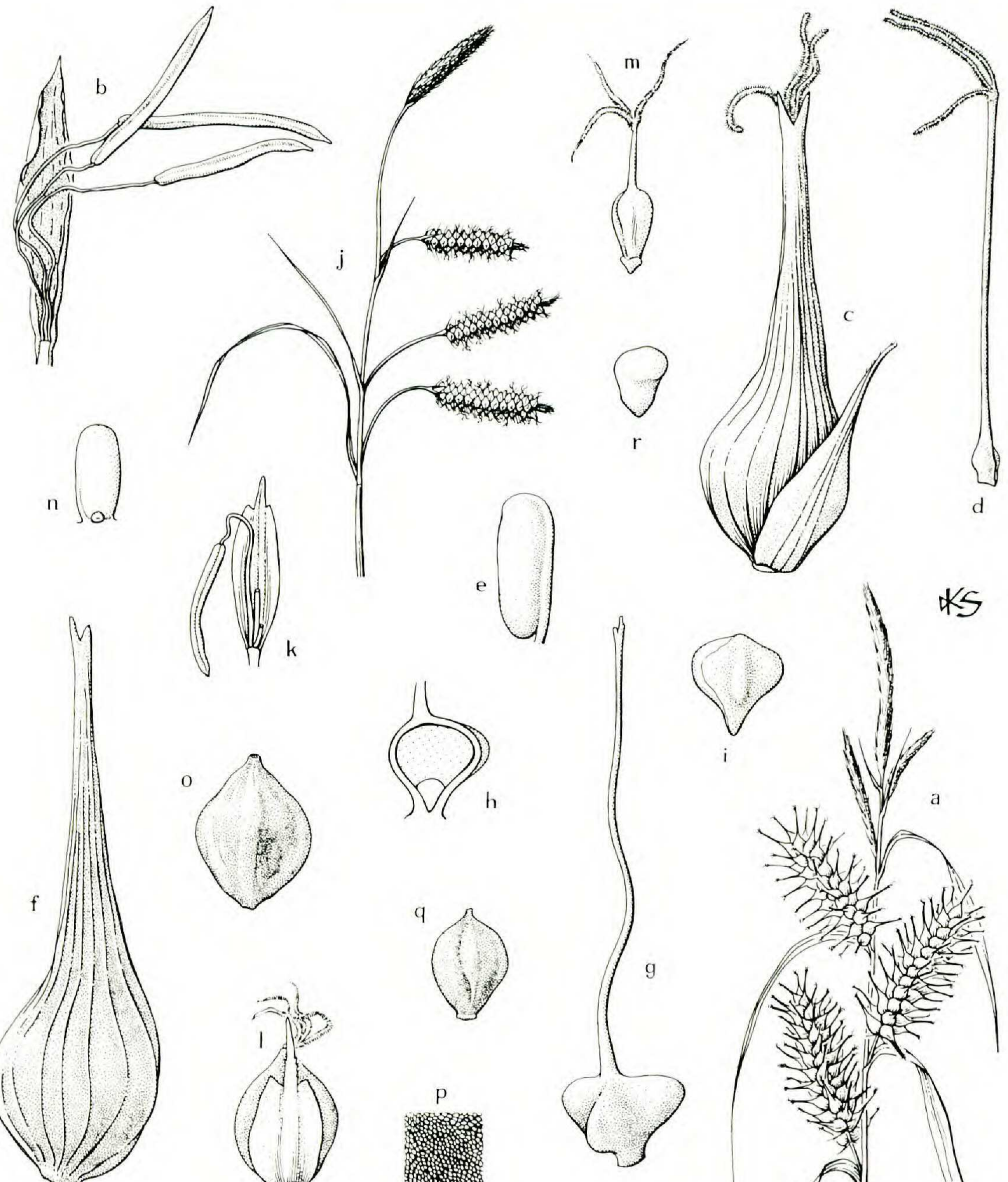

FIGURE 6. *Carex* subg. CAREX (subg. *Eucarex*). a–i, *C. gigantea:* a, inflorescence, uppermost 3 spikes staminate, × ½; b, staminate flower and subtending scale, adaxial view, × 5; c, perigynium in axil of subtending scale, stigmas of carpellate flower protruding, × 5; d, carpellate flower (gynoecium), perigynium removed, × 5; e, ovule, lateral view, micropyle not visible, × 25; f, mature perigynium enclosing achene, × 5; g, achene with persistent style, × 5; h, longitudinal section of achene, seed coat not shown, embryo basal, endosperm above, × 5; i, seed removed from achene, × 5. j–r, *C. glaucescens:* j, inflorescence, staminate spike uppermost, × ½; k, staminate flower and subtending scale, most of 2 stamens removed, × 5; l, perigynium and subtending scale, stigmas of carpellate flower protruding, × 5; m, carpellate flower, × 5; n, ovule, micropyle visible, raphe behind, × 25; o, mature perigynium enclosing achene, × 5; p, perigynium, detail of surface, showing globular to ellipsoid cells that produce glaucous effect, × 25; q, achene, × 5; r, embryo, × 25.

infestations of smut fungi, indicated a probable close relationship with subfam. Rhynchosporoideae; Koyama concurred with this opinion. A clearer understanding of generic relationships of the genus must await a better picture of evolution within the genus. Its very large size and worldwide distribution continue to hamper such studies.

Kükenthal believed that subg. PRIMOCAREX Kükenthal was the most primitive within the genus. A succession of more recent cyperologists (Kreczetowicz; Nelmes; Koyama, 1962a; Le Cohu, 1968; Haines & Lye; Smith & Faulkner; Reznicek, 1986b) have taken the opposite view. In their opinion the unispicate condition of subg. PRIMOCAREX was derived (perhaps polyphyletically) from ancestors with richly branched inflorescences like those of subg. INDOCAREX. However, the presence of a rachilla within the perigynium of some species of subg. PRIMOCAREX suggests that it is the most primitive subgenus. Smith & Faulkner believed that subgenera CAREX and VIGNEA might have evolved from subg. INDOCAREX by reduction in inflorescence structure (a pattern also suggested for several other genera of the family, e.g., *Cyperus* and *Scirpus*). This would have involved loss of cladoprophylls (tubular prophylls subtending branches) and reduction of branching. There are contrasting interpretations of the inter- and infrageneric relationships in *Carex*.

The morphology of the inflorescences, particularly of the spikes and perigynia, has traditionally been most heavily relied upon in distinguishing species and circumscribing sections. Anatomical and cytological features are also taxonomically useful. Anatomical evidence has long been applied to the systematics of *Carex*. Crawford described the stems and leaf blades of the British species. Akiyama presented a systematic study of the eastern Asian species, emphasizing anatomical differences. Several recent revisions have included anatomical descriptions of culms and leaves. Standley (1985a), in her monograph of the northwestern species of sect. PHACOCYSTIS Dum. (sect. *Acutae*), showed that related species differ in the distribution of sclerenchyma and stomata in culms and leaf blades. In certain species stomata are present on one or both surfaces (Standley, 1986). The importance of anatomical features has also been discussed by Le Cohu (1972) and by Metcalfe.

Recent studies with the scanning electron microscope have revealed an interesting variety of surface features in leaves, perigynia, and achenes of *Carex*. The presence of tubercles (Hoshino, 1986) and papillae (Maloney & Evans) and the distribution of stomata (Standley, 1986) are useful in distinguishing species and circumscribing sections.

Cytological studies have been helpful in *Carex,* but chiefly at the specific level. Chromosome numbers in the genus range from $n = 6$ to $n = 56$. The base chromosome number is 5, and the commonest haploid numbers in North American species are 10, 20, 30, and 40 (Wahl). In many instances related pairs of species differ in chromosome number. Aneuploidy is prevalent within the genus. Aneuploid series characterize many sections (Wahl; Davies; Dietrich; Faulkner, 1972). Polyploidy is infrequent.

The pollination biology of *Carex* has received little attention. Most species are anemophilous. Honey bees and beetles visit inflorescences to gather pollen

and thus may also be vectors (Leppik). Self-compatible and self-incompatible species have been noted in the genus (Faulkner, 1973; Handel, 1976, 1978a; Schmid, 1984b). It is not known whether the incompatibility is sporophytic or gametophytic. Handel (1976) determined that pollen-flow distances in *C. platyphylla* Carey and *C. plantaginea* Lam. were rarely more than 10 m.

Little is documented about the dispersal of fruits of *Carex*. It has been assumed that species with inflated perigynia are dispersed by floating on water, but experimental verification is lacking. Several North American species (e.g., *C. communis* Bailey, *C. umbellata* Willd., and *C. pedunculata* Willd.) have elaiosomes at the base of the perigynia and are dispersed by ants (Handel, 1978; Gaddy, 1986). *Carex pauciflora* Michx., widespread in northeastern North America, has subulate perigynia that at maturity spring away from the rachis (up to 60 cm) when touched (Hutton).

Flavonoid profiles can be used to distinguish between closely related species. Toivonen (1974) showed this in the Fennoscandian representatives of sect. CANESCENTES (sect. *Heleonastes*). Manhart (1985) demonstrated that classifications based on occurrences of flavonoids were similar to relationships determined by morphology.

The species of *Carex* fall into three broad ecological groups with regard to habitat: wetland, forest, and ruderal. In general the species of a section are ecologically similar. Several sections (e.g., sects. PALUDOSAE G. Don and LUPULINAE Carey) include mostly wetland species. Section ACROCYSTIS Dumort., however, contains species of dry to dry-mesic open or wooded habitats. Several sections (e.g., sect. ALBAE Ascherson & Graebner) are composed mostly of calcicoles.

Most species of *Carex* are rhizomatous perennials. *Carex* is the only large genus of the family containing no annuals. Certain species reproduce mostly vegetatively (e.g., *C. Bigelowii* Torrey, plants of which set abundant seed, with little germination or recruitment of seedlings unless disturbance occurs). In the boreal *C. flava* L. seedlings persist for several years until competition is removed (by disturbance or herbivory) and then grow rapidly to fill in the available space (Schmid, 1986).

The economic importance of the genus lies chiefly in providing fodder for domestic and wild mammals, especially in colder regions. Many Russian species are important in this way (Goncharov *et al.*); *Carex stans* Drejer and *C. discolor* Nylander provide good grazing for cattle and reindeer. In Iceland, meadows of *C. Lyngbyei* Hornem. are managed and yield up to five tons per hectare. The nutritional content is very similar to that of common pasture grasses such as Kentucky bluegrass, *Poa pratensis* L.

The following is a synopsis of the southeastern species, with chromosomal, systematic, and ecological references. The order and circumscription of sections generally follows Mackenzie (1931–1935).

Subgenus VIGNEA (Lestib.) Kükenthal, represented in the Southeast by species belonging to ten sections, is characterized by lenticular achenes, dorsiventrally flattened perigynia, two stigmas, and both carpellate and staminate flowers in each spike of the inflorescence.

Species of sect. AMMOGLOCHIN Dumort. (*Arenariae* Kunth, including sect.

Divisae) are small rhizomatous plants of grasslands and strands. Two Eurasian species, *Carex arenaria* L., $n = 29, 58, 60, 64$ (Noble) and *C. divisa* Hudson, are naturalized in our area. Both grow on coastal sands from eastern Maryland to eastern North Carolina. Several others occur in Canada and the western United States, where *C. Eleocharis* Bailey is an important forage in the Rocky Mountain region (Hermann, 1970).

Section MACROCEPHALAE Kükenthal comprises two eastern Asian species, one of which, *Carex Kobomugi* Ohwi, $2n = 84, 88$, is sparingly naturalized from eastern Virginia (Norfolk Co.) north to Cape Cod; it should be looked for in eastern North Carolina. Standley (1985b) studied its population biology. Although previous authors had described the species as dioecious, she showed that individual rhizomes of a clone were consistently either staminate or carpellate (monoecious).

Section PHAESTOGLOCHIN Dumort. (sect. *Bracteosae* (Kunth) Pax) is one of the most diverse sections of *Carex* in North America; it includes 16 species in our area, all with ranges that extend into the northeastern United States or to Canada. Plants of these species are mostly caespitose, with one to five sessile androgynous spikes. Webber & Ball revised the *C. rosea* complex and corrected the application of the names *C. rosea* and *C. convoluta*. Chromosome numbers are known for six southeastern representatives of this section: *C. sparganioides* Muhl., $n = 23$; *C. cephalophora* Muhl. ex Willd., $n = 24$; *C. retroflexa* Willd., $n = 20$; *C. rosea* Schkuhr (*C. convoluta* Mack.), $n = 26$; *C. appalachica* Webber & Ball (*C. radiata* auct., non (Wahlenb.) Sm.); and *C. radiata* (Wahlenb.) Small (*C. rosea* auct., non Schkuhr), $n = 29$. David & Kelcey summarized the biology of the European species, *C. muricata* L., *C. spicata* Hudson, and *C. divulsa* Stokes, all $2n = 58$. *Carex spicata* and *C. divulsa* are naturalized in the Northeast south to Virginia. They might be found in North Carolina.

Section MULTIFLORAE (Kunth) Mack. contains three species in our area. The commonest of these, *Carex vulpinoidea* Michx., $n = 26, 27$, is known from all of the southeastern states and ranges north into southern Canada. It is also sparingly naturalized in England (Clapham *et al.*). The other southeastern species are *C. triangularis* Boeck. and *C. annectens* Bickn. Both occur in most of the southeastern states, but neither is as common as *C. vulpinoidea*.

Section HELEOGLOCHIN Dumort. (sect. *Paniculatae* G. Don (Hort. Brit. 367. 1830; non Carey) is represented in the Southeast by *Carex decomposita* Muhl., $n = 30, 32, 33$, which occurs in every state in our area. Plants of this section are the only North American representatives of *Carex* with paniculate inflorescences. Certain extraregional species of the section appear to be cytologically conservative (cf. Clapham *et al.*). *Carex diandra* Schrank, $2n = 60$, is circumboreal, while *C. paniculata* L., $2n = 60, 62, 64$, and *C. appropinquata* Schum., $2n = 64$, are European.

In the Southeast, sect. VULPINAE (Carey) Christ is represented by five species of swamps, marshes, and wet meadows. The plants resemble those of the preceding two sections but are distinguished by their long, slender perigynia (1 cm long in *Carex crus-corvi* Shuttlew.). In several species the bases of the perigynia are conspicuously enlarged with aerenchyma, which probably makes the fruits buoyant and allows dispersal by water. *Carex crus-corvi*, $n = 26$, *C.*

laevivaginata (Kükenthal) Mack., $n = 23$, and *C. stipata* Willd., $n = 26$, occur throughout our area.

Section GLAREOSAE G. Don (sect. *Heleonastes* (Kunth) Kükenthal) is a group of circumboreal species of wet woods and bogs. The plants are small and have few-flowered inflorescences. Three species, *Carex brunnescens* subsp. *sphaerostachya* (Tuckerman) Kalela, $n = 27, 28$, *C. canescens* L., $n = 27, 28$, and *C. trisperma* Dewey, $n = 30$, barely reach our area from the north and are found in the mountains of North Carolina and Tennessee.

Section STELLULATAE (Kunth) Christ consists of perhaps 30 species worldwide. The plants are caespitose and have gynecandrous spikes of spreading to reflexed perigynia with serrulate beaks. Reznicek & Ball (1980) revised the North American species and provided excellent keys and descriptions. There are seven representatives in our area. *Carex Ruthii* Mack. is endemic to high elevations in the southern Appalachian Mountains from West Virginia to Georgia. *Carex exilis* Dewey is primarily northeastern, occurring from Newfoundland to Ontario south to Maryland; it is also known from widely disjunct stations in central North Carolina, southern Mississippi, and southern Alabama. The other southeastern species are *C. atlantica* Bailey (including *C. Mohriana* Mack.), *C. Howei* Mack., $n = 27$, *C. incomperta* Bickn., $n = 22$, and *C. angustior* Mack., $n = 26$. The two European species for which counts are available have similar numbers: *C. elongata* L., $2n = 56$, and *C. echinata* Murray, $2n = 56, 58$.

Species of sect. DEWEYANAE (Tuckerman) Mack. are probably closely related to those of sect. STELLULATAE but have fewer, narrower, and appressed rather than spreading perigynia (Reznicek & Ball, 1980). *Carex bromoides* Schkuhr, $n = 31+(4)$, is the sole southeastern representative; it occurs in every state in our area. *Carex Deweyana* Schwein., the only other species of the section, occurs in northeastern North America.

Section OVALES (Kunth) Christ contains about 50 species in North America. It is the largest section in our area, and the 16 representatives occurring in the Southeast have flattened, papery, appressed perigynia in dense, ovoid spikes. The section is taxonomically difficult and needs revisionary work. Several taxa recognized by Mackenzie (1931–1935) have been synonymized by later workers. Most of our species are widespread in eastern North America. For example, *Carex tribuloides* Wahlenb., $n = 35$, and *C. reniformis* (Bailey) Small occur in all the southeastern States, while *C. argyrantha* Tuckerman and *C. aenea* Fern. are northeastern and just enter our area in the mountains of North Carolina. *Carex vexans* Herm. is endemic to central and southern Florida. Among our representatives, chromosome numbers are known only for *C. tenera* Dewey ($n = 26, 27, 28$), *C. straminea* Willd. ($n = 34+(3)$), and *C. cristatella* Mack. ($n = 35$). The type species, the European *C. ovalis* Good., $2n = 64, 66, 68$, is cytologically similar to eastern North American species of the section.

Subgenus CAREX (subg. *Eucarex* Cosson & Germ.) includes the remaining sections of the genus, 26 of which are represented in the Southeast. The plants are characterized by differentiated spikes in which the terminal spike is wholly staminate and the others are wholly or partly carpellate. Except in the distig-

matic sect. PHACOCYSTIS Dumort. (sect. *Acutae*), the ovaries and achenes are trigonous and there are three stigmas.

Section POLYTRICHOIDEAE (Tuckerman) Mack. contains only *Carex leptalea* Wahlenb., $n = 26$, an eastern North American endemic growing in damp, mossy woods, often in calcareous soils, from Florida and eastern Texas north into Canada. These are small, thin plants bearing few slender, beakless perigynia and narrowly oblong, truncate achenes.

Section PHYLLOSTACHYAE (Tuckerman) Bailey has four North American species, characterized by androgynous spikes and staminate scales with basally fused margins. Two, *C. Jamesii* Schwein., $n = 35$, and *C. Willdenovii* Schkuhr, $n = 31$, occur in the Southeast. In addition to features of the perigynia, these species are distinguished by the distribution of micropapillae on the leaves and culms (Maloney & Evans).

Section ACROCYSTIS Dumort. (*Montanae* (Kunth) Carey) comprises ten species in the Southeast and nearly 30 worldwide. The plants grow in the most xeric habitats of any species of *Carex* in our area, typically dry woodlands and rock outcrops. They are small and tufted, with the leaves stiff, the carpellate spikes few flowered, and the perigynia globose to ovoid, closely covering the roundly trigonous achenes. Chromosome numbers are reported for half of our representatives and indicate an aneuploid series: *C. communis* Bailey, $n = 14$, *C. nigromarginata* Schwein., $n = 17$, *C. artitecta* Mack., $n = 18$, *C. pensylvanica* Lam., $n = 18$, and *C. lucorum* Willd. ex Link, $n = 20$. The European species are more diverse cytologically ($n = 9, 15, 19, 33$) but are similar ecologically. The fruits of *C. artitecta* (Handel, 1978) and *C. nigromarginata* (Gaddy, 1986) are dispersed by ants.

Section PICTAE Kükenthal has two representatives in eastern North America, *Carex picta* Steudel and *C. Baltzellii* Chapman ex Dewey. Both are local, dry-woodland species of the unglaciated eastern United States. *Carex Baltzellii* is endemic to Georgia and northern Florida. *Carex picta*, occurring from southern Indiana to Georgia and Louisiana, is a curious species. It is the only native dioecious representative of *Carex* in our area. The plants form "fairy rings" as the rhizomes branch and proliferate dichotomously (see Martens for illustration). Clones from individual rhizomes are consistently staminate or carpellate, and carpellate plants do not always flower every year.

Section CLANDESTINAE G. Don (*Digitatae* (Fries) Carey) consists of four species of the North Temperate Zone. The plants have purple leaf sheaths and perigynia with minute beaks and tapered bases. *Carex pedunculata* Muhl., which grows on wooded, mesic, calcareous slopes, is the only representative of the section in the Southeast. Elaiosomes are borne at the base of the perigynia, which are dispersed by ants (Handel, 1976; Gaddy, 1986). Mackenzie (1931–1935) included the only tetrastigmatic species of *Carex, C. concinnoides* Mack. of the Pacific Northwest, in this section. St. John & Parker established subg. *Altericarex* for this unusual species, but aside from its tetramerous carpellate flowers, *C. concinnoides* fits in sect. CLANDESTINAE rather well, both morphologically and ecologically.

Section TRIQUETRAE (Carey) Kükenthal comprises five species of temperate

North America. The plants are caespitose, and they have greenish sheaths and short-beaked, pubescent perigynia. There are two representatives in the Southeast, *Carex dasycarpa* Muhl. and *C. tenax* Chapman ex Dewey. Both grow in pine forests, mostly from South Carolina to southern Mississippi. Another species of the section, *C. hirtifolia* Mack., $n = 22+(3)+(3)$, of the northeastern United States, reaches its southern limit in the mountains of Virginia.

Section ALBAE Ascherson & Graebner consists of two species, both boreal calcicoles of dry soils. One of these, *Carex eburnea* Boott, the only North American representative, is a stoloniferous plant with glabrous perigynia that is recorded in our area only from Tennessee. The second is *C. alba* Scop., $2n = 54$, of Eurasia.

Section PANICEAE G. Don (non Christ) is a Eurasian and North American section of 12 species, five of which occur in the Southeast. The stoloniferous plants have purple to reddish scales subtending the flowers, and ascending to spreading, more or less ovoid perigynia. A member of this section, the rare southern Appalachian endemic *Carex Biltmoreana* Mack., occurs on wet, shaded cliffs in the Blue Ridge Mountains of North and South Carolina (Gaddy, 1983). Three of our representatives, *C. Woodii* Dewey, $n = 22, 26$, *C. tetanica* Schkuhr, $n = 26$, and *C. Meadii* Dewey, are mostly northern in distribution and just reach our area in the mountains of Tennessee and North Carolina. The fifth species, *C. Chapmanii* Steudel, is endemic to the Coastal Plain between Florida and North Carolina. The European *C. panicea* L. and *C. vaginata* Tausch have lower chromosome numbers: both are $2n = 32$.

Section LAXIFLORAE (Kunth) Kükenthal, containing about 25 species in eastern North America (17 in our area), one in the western United States, and a few in eastern Asia, is the most diverse section of *Carex* in our area. The plants grow in woodlands; they are caespitose and bear conspicuously two-nerved perigynia. Our species have recently been studied by Bryson, and Manhart (1986) has investigated their cytology. Handel (1978a), who investigated the pollination biology of *Carex plantaginea* Lam. and *C. platyphylla* Carey, reported that both are self-compatible and that apomixis is absent. He studied the dispersal of pollen by wind and found that pollen was transported twice as far from *C. plantaginea* as from *C. platyphylla*. This difference was attributed to the greater average height above ground of the staminate flowers in *C. plantaginea*. An aneuploid series is evident in those southeastern representatives of the section for which chromosome numbers have been reported: *C. Manhartii* Bryson, $n = 14$, *C. purpurifera* Mack., $n = 17, 18, 19$, *C. leptonervia* (Fern.) Fern., $n = 18, 19$, *C. blanda* Dewey, $n = 18, 19, 20, 21, 22$, *C. gracilescens* Steudel, $n = 20$, *C. laxiflora* Lam., $n = 20$, *C. laxiculmis* Schwein., $n = 22, 23$, *C. digitalis* Willd., $n = 24$, *C. plantaginea*, $n = 25$, and *C. platyphylla*, $n = 33, 34, 35$. *Carex striatula* Michx. and *C. laxiflora* are myrmecochorous (Gaddy, 1986).

Section GRANULARES (O. F. Lang) Kükenthal includes five eastern North American species, of which four are found in the Southeast. They are calcicoles and have few-flowered pedunculate spikes and perigynia with many fine nerves. *Carex granularis* Muhl. ex Willd., $n = 16+(4)$, occurs in all the southeastern states and is the widest-ranging species of the section. The other southeastern

representatives are *C. rectior* Mack., *C. Crawei* Dewey, and *C. microdonta* Torrey & Hooker.

To sect. OLIGOCARPAE (Carey) Kükenthal (including sect. *Griseae* Bailey) belong nine species of eastern North America, of which six are present in our area. Members of this section are ecologically and morphologically similar to plants of sect. GRANULARES but have lower chomosome numbers. *Carex flacosperma* Dewey (*C. glaucodea* Tuckerman), *C. oligocarpa* Schkuhr, $n = 27$, and *C. grisea* Wahlenb. (*C. corrugata* Fern.), $n = 28$, occur nearly throughout our area and are also found in the northeastern United States.

Species of sect. HYMENOCHLAENAE (Drejer) Bailey (including sects. *Sylvaticae* Boott and *Gracillimae* (Carey) Kükenthal) are widely distributed in the temperate regions of the Northern Hemisphere and in the East African Highlands (Kükenthal; Mackenzie, 1931–1935). The plants have slender, drooping spikes and often strongly beaked perigynia. A European representative of this section, *Carex sylvatica* Hudson, $2n = 58$, is naturalized in southern New England and Long Island. There are six species in the Southeast. The eastern North American representatives are currently being revised (with particular attention to cytology) by Waterway (in prep.). Reznicek (1986a) has provided a detailed illustrated study of the Mesoamerican species. Chromosome numbers have been reported for *C. gracillima* Schwein. ($n = 5, 27$), *C. flexuosa* Muhl. ex Willd. ($n = 27, 28$), *C. aestivalis* Curtis ($n = 28$), and *C. prasina* Wahlenb. ($n = 30$), all of which occur in the Southeast. *Carex cherokeensis* Schwein., wolf-tail, reported from every state in the Southeast, and *C. Sprengelii* Dewey, $n = 21$, of the northeastern United States, are sometimes segregated into sect. *Longirostres* Kükenthal because of their longer perigynial beaks.

Section VIRESCENTES (Kunth) Carey is represented in temperate North America, Eurasia, and the mountains of northern South America. The plants have densely cylindrical, stiffly erect spikes. There are six species in eastern North America, and all occur in the Southeast. Our representatives for which chromosome numbers are known (*Carex Bushii* Mack., $n = 24$, *C. hirsutella* Mack., $n = 26$, *C. Swanii* (Fern.) Mack., $n = 27$, and *C. virescens* Muhl. ex Willd., $n = 30$) provide yet another example of the aneuploidy so frequent in the genus.

Species of sect. CAREX (sect. *Hirtae* (Tuckerman) Christ) are widespread in the Northern Hemisphere, and a few are disjuncts in temperate South America. The plants are stoloniferous and have three to ten spikes of ascending, ovoid perigynia. The section has only two representatives in the Southeast: the Northeastern and midwestern *Carex lanuginosa* Michx., $n = 39$, is known in our area only from Arkansas, while *C. striata* Michx. (non *C. striata* Gilib., *nom. illeg.*; *C. Walteriana* Bailey), of the Coastal Plain, ranges from Georgia north to southeastern Massachusetts. The type species of this section and of the genus, *C. hirta* L., $n = 56$, is sparingly adventive in the northeastern United States (south to the District of Columbia).

Section ANOMALAE Carey includes many species in eastern Asia and Australasia, one in the western United States, and another in the eastern United States, *Carex scabrata* Schwein., $n = 27$, recorded in our area from North Carolina, Tennessee, and northern Alabama. Plants of this species have dense,

cylindrical carpellate spikes and perigynia with bidentate beaks; they are stoloniferous and typically grow near woodland springs.

The monotypic sect. SHORTIANAE (Bailey) Kükenthal contains *Carex Shortiana* Dewey, an uncommon but attractive species of the Ohio River valley south to central Tennessee. The plants have culms each bearing four or five gynecandrous spikes of nerveless, corrugated perigynia with stipitate bases and entire beaks.

The species of sect. PENDULINAE (Fries) Christ have a circumpolar distribution and are characterized by pedunculate spikes and closely spaced perigynia. The type species is the European *Carex pendula* Hudson, $2n = 58$ or 60. The three representatives in our area, *C. Joorii* Bailey, *C. verrucosa* Muhl., and *C. glaucescens* Ell., are all widely distributed.

Species of sect. LIMOSAE (Tuckerman) Christ have drooping, few-flowered spikes and broadly elliptic, beakless perigynia. Many are circumboreal in distribution and grow in fens, bogs, or wet woods. A single, primarily northeastern representative, *Carex Barrattii* Schwein. & Torrey, from the mountains of Tennessee and North Carolina, is known in our area. The type species is the circumboreal *C. limosa* L., $2n = 56$.

The diverse and heterogeneous sect. ATRATAE (Kunth) Christ[19] contains many species of the arctic and alpine tundra. The plants are characterized by sessile, erect or drooping spikes, dark pistillate scales, and beaked or beakless perigynia. There are many representatives in the southern Rocky Mountains (Hermann, 1970; Murray), but none of these is shared with our area. The single species of our area, *Carex Buxbaumii* Wahlenb., $n = 37$, ca. 50, reaches its southern limit in North Carolina and Arkansas.

Section PHACOCYSTIS Dumort. (sect. *Acutae* Fries) is also a diverse circumboreal group. The plants are moderately large and have drooping spikes and distigmatic, lenticular achenes. Three northeastern species, *Carex strictior* Dewey, $n = 34$, *C. stricta* Lam., and *C. torta* Boott ex Carey, $n = 33$, reach their southern limits in the northern half of our area. Standley (1985a) revised the 15 representatives of this section in the Pacific Northwest. While none of the species she treated occurs in our area, her thorough investigation of interspecific differences in leaf and culm anatomy, cytology, morphology, and some aspects of ecology is informative and provides a model for future studies.

Species of sect. CRYPTOCARPAE (Tuckerman) Kükenthal are mostly wetland plants. They have drooping, densely flowered spikes and trigonous achenes. *Carex gynandra* Schwein., *C. Mitchelliana* M. A. Curtis, and *C. crinita* Lam., $n = 33$, occur in the Southeast. These have been treated as a single taxon under the last name, but there is good evidence for their specific status (Bruederle & Fairbrothers, 1986). *Carex gynandra* and *C. crinita* hybridize rarely. The hybrids produce aborted achenes (Standley, 1983).

Section COLLINSIAE Mack. contains a single species, *Carex Collinsii* Nutt., that grows in swamps on the Atlantic Coastal Plain from Georgia to Rhode

[19] *Carex* sect. ATRATAE (Kunth) Christ, Bull. Soc. Bot. Belg. **24:** 15. 1885.

Island (Tucker, 1978). It is characterized by few-flowered inflorescences and subulate perigynia.

Species of sect. FOLLICULATAE Mack. also have subulate perigynia, but the spikes are densely many flowered and the plants are taller. There are two representatives in the Southeast, *Carex lonchocarpa* Willd. ex Sprengel, found throughout our area, and *C. folliculata* L., $n = 28$, a northeastern species growing only in the mountains of North Carolina and Tennessee.

Species of sect. PSEUDO-CYPEREAE (Tuckerman) Christ are tall, paludal plants of circumpolar distribution. They have drooping, slenderly cylindrical spikes and densely arranged, conspicuously bidentate perigynia. There are two representatives in our area, *Carex Schweinitzii* Dewey, $n = 30$, and *C. comosa* Boott, $n = 32$. *Carex pseudocyperus* L., $2n = 66$, is widespread in the Northern Hemisphere and is believed to be native to New Zealand (Clapham *et al.*).

Section PALUDOSAE G. Don[20] has eight species in North America and several in Eurasia. The plants are stoloniferous and bear firm, many-nerved, slightly inflated perigynia. There are two representatives in our area, *Carex hyalinolepis* Steudel, found in wetlands throughout the Southeast, and *C. trichocarpa* Muhl. ex Schkuhr, $n = 55$, a boreal bog species known in the Southeast only from the mountains of North Carolina (Core).

Dense spikes of conspicuously inflated perigynia characterize members of sect. SQUARROSAE Carey, which are endemic to eastern North America. There are three species in our area, *Carex Frankii* Steudel, *C. typhina* Michx., and *C. squarrosa* L., $n = 28$, each occurring in all or most of the southeastern states.

Section VESICARIAE (Tuckerman) Carey is a group of perhaps 20 species, mostly of eastern North America and Eurasia. The plants generally grow in shallow water and are characterized by inflated perigynia. Five representatives occur in our area, but only one, *Carex lurida* Wahlenb., $n = 32, 33$, is common (reported from every state). The others are *C. Baileyi* Britton, $n = 34$, *C. bullata* Schkuhr, *C. Elliottii* Schwein. & Torrey, and *C. rostrata* Stokes, $n = 34$. The type species, *C. vesicaria* L., $n = 41$, and *C. riparia* Curtis, $n = 36$, are cytologically similar Eurasian representatives.

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Under *Rhynchospora* see LEPPIK.

Under *Cymophyllus* see KÜKENTHAL; MACKENZIE (1931–1935).

[20]*Carex* sect. PALUDOSAE G. Don in Loudon, Hort. Brit. 367. 1830, non (Fries) Christ (1884). TYPE SPECIES: *C. paludosa* Good. (= *C. acutiformis* Ehrh.).

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